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THE CONDOR

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SEX AND AGE CHARACTERS AND SALIVARY GLANDS OF THE CHIMNEY SWIFT

By DAVID W. JOHNSTON

In the spring of 1955, an investigation was begun on the salivary glands of the Chimney Swift (*Chaetura pelagica*). Emphasis was to be placed on the growth and development of these glands seasonally, and comparisons and correlations were to be made between their macroscopic and microscopic appearance and other anatomical, biological, and reproductive features of this species. In the interim, Marshall and Folley published a significant paper (1956) concerning several of these same aspects in swiftlets (*Collocalia* spp.), whose gelatinous nests have been consumed by humans for centuries because of their nutritional values. The basis for their paper was the histologic structure of the glands of only two birds, and, using their findings as a guide for continuing the present study, I amassed additional data to give a more complete understanding of the salivary gland development in another species.

This investigation was started as a "simple" study of salivary glands, but as the work progressed it became apparent that many aspects of the life history of the Chimney Swift, such as sex and age characters and molt, were largely unavailable in the literature. It was necessary, then, to work out these "peripheral problems" in some detail before the salivary gland study could be completed. Thus, some of the following data seem unrelated to salivary glands at first glance, but they are presented here because (1) a complete understanding of these additional morphological, anatomical, and biological details permits an accurate interpretation of the biology and physiology of the salivary gland, and (2) these data, although incomplete in certain refinements, represent significant contributions to the published, extant data on the life history of the Chimney Swift.

MATERIALS AND METHODS

Seventy-five Chimney Swifts were collected from 1955 through 1957 in central Georgia and South Carolina where this species is a common summer resident and an abundant fall migrant. Most of the birds were shot between 6 p.m. and dark, and they were either dissected immediately, frozen in aluminum foil, or preserved whole in Bouin's fixative. The majority of the swifts were taken near Macon, Bibb County, Georgia, but approximately five per cent of the total came from each of the following localities: Athens, Clarke County; Oglethorpe, Macon County; and Sandersville, Washington County, Georgia, and the Savannah River Plant, Aiken County, South Carolina. In 1955, 18 swifts were collected, in 1956, 38, and in 1957, 19. As the accompanying tables and figures will show, the birds were taken from mid-April until mid-October, with the individual dates of collection being rather uniformly spread throughout this period (see table 1).

After weighing the birds not fixed in Bouin's solution, examining them for molt, and dissecting them for sex and age determination, I decapitated each bird, plucked the head, and slit the skin under the mouth so that the fixative might penetrate the salivary glands rapidly and completely. These heads, bearing appropriate collection numbers, were then fixed in Bouin's solution so that, at a later time, the glands could be measured,

weighed, and/or sectioned. Not all of the heads were fixed quickly enough to be suitable for histologic work.

SEX AND AGE DIFFERENCES

A few attempts have been made by banders of Chimney Swifts to determine correctly the sex and age of live swifts, but the suspected external differences have usually proven to be relative and, with the possible exception of molting birds in the late summer and early fall, largely ineffective in completely accurate separation of sex and age groups of live birds. Since the present study involved freshly-killed birds, it was possible to look for internal characters as well as external ones, and by applying these characters singly or in various combinations, the ages of swifts could be determined accurately at least insofar as birds-of-the-year versus adults was concerned. In the spring and early summer, however, one-year-olds were indistinguishable from older birds both internally and externally. For sex and age differences the following characters were studied: weight, molt, skull ossification, the bursa of Fabricius, and gonadal development.

Weight.—Although thousands of Chimney Swifts have been handled by banders, very few weights are available for this species primarily because only by dissection can one correlate accurately age and sex with weight. The Lacks (1951:505 ff) give weights for many adult *Apus apus*, but these data do not distinguish between weights of the sexes. The data presented in table 1 represent more seasonal weights of definitely-aged and -sexed Chimney Swifts than had been recorded previously (Fischer, MS), but Dexter (1957) has recently weighed 119 Chimney Swifts killed accidentally on May 20, 1956, in Ohio. Most of the birds in my sample were taken late in the afternoon or early evening at a time when one would expect a maximum diurnal weight, and in several birds of this sample the mouth cavity was packed with small insects as was also the gizzard. After each bird was shot it was carefully wrapped in foil to prevent weight loss. Usually within an hour each bird was weighed to the nearest tenth of a gram.

Table 1

Weights of Adult Chimney Swifts, Taken in Central Georgia and South Carolina, 1955–1957

	Males			Females		
Date	Number	Mean	Range	Number	Mean	Range
Apr. 16–30	4	25.2	24.1–27.1	2	24.2	23.4–25.0
May 1–15						
May 16–31	3	22.8	20.0–25.6	3	24.7	23.3–27.5
June 1–15	4	23.3	21.7–24.5	2	22.1	21.6–22.5
June 16–30	3	22.8	21.8–24.3			
July 1–15	4	22.2	20.7–23.1	4	21.2	19.8–22.3
July 16–31	1	23.1		2	21.9	21.5–22.3
Aug. 1–15				1	20.3	
Aug. 16–31	3	22.7	22.1–23.6	3	22.6	21.4–23.5
Sept. 1–15						
Sept. 16–30				1	23.3	
Oct. 1–15	3	29.9	28.3–31.7	2	30.4	30.4

In the Chimney Swift, the data in table 1 indicate that for both sexes the heaviest birds are found in the spring and fall whereas during the actual period of breeding and in late summer, the birds are lightest in weight. A similar situation was found in *Apus* by the Lacks. For the Chimney Swift this statement can be explained, at least in part, by the degree of relative fatness of each bird. My own subjective impressions of birds taken in April was that the birds were "moderately fat," those taken in June had "no

fat," and those taken in July and August had "some fat." The few birds collected in October were termed "very fat." Quite noticeable, then, were the extremely heavy birds in October, birds which, upon dissection, proved to be the fattest of any examined.

Weights of immatures (principally non-molting birds, taken from large flocks of adults and immatures) do not differ significantly from those of adults collected at the same time. Weight data for three immature males are 22.8 grams (Aug. 28), 22.1 (Aug. 29), and 23.0 (Sept. 3). Four immature females weighed 23.0 (July 14), 21.7 (July 26), 23.7 (Aug. 23), and 24.9 (Oct. 5). Even in this small sample there was some tendency for the heaviest birds to be found later in the season.

Fischer (MS) found that in a given pair, weighed several times during and after the breeding season, the female weighed more than the male by approximately one gram. In one year (1951) this pair lost weight in the course of the summer, but in the following year a weight loss in summer was less evident. The sex of Fischer's birds was determined by the observer primarily on the basis of behavior. Other data presented by Fischer (twelve specimens taken in May at Ithaca, New York) showed that males tend to outweigh females. Similarly, Dexter (1957) found that 60 males ranged in weight from 21.5 to 27.5 grams with an average of 24.6, and 59 females ranged in weight from 21.5 to 28.0 grams with an average of 24.3. The average weight of 26 adult males from table 1 is 24.0 grams whereas the average weight of 20 adult females is 23.4. Since these data represent a much larger sample than had been available previously for the Chimney Swift, it seems reasonable to assert that on the average (1) males tend to outweigh females, although the difference is not significant statistically and could not be used reliably to distinguish sexes, and (2) in midsummer, birds of both sexes weigh less than they do in either the spring or fall at the latitude of central Georgia. This latter condition is believed to be correlated closely with fat deposits.

Molt.—With the exception of the meager data given by Bent (1940:277–278) I have been unable to locate specific details on molt in the Chimney Swift. Therefore, the following description of molt is presented in some detail so that certain aspects of the molt might be used in age determination. Ben B. Coffey, Jr., advises me (personal correspondence) that banders for many years have distinguished adult Chimney Swifts in the fall from immatures by the fact that the adults were molting and the immatures were not. Toward the end of the molting period (September), however, the accuracy of this method decreases because some adults might complete their postnuptial molt by mid-September. As will be discussed below, the degree of skull ossification indicates that the use of molt to denote an adult is reliable in ascertaining the age of a given swift up to a given time.

The first indication of the postnuptial molt in the adult is the loss of primary number one and its covert. Thereafter, the essential salient features of molt are summarized in figure 1. Aside from these sequences of molt, it is also necessary to indicate that the greater secondary coverts are replaced before the secondaries begin their molt, and that the upper and lower tail coverts molt before the rectrices. It is not uncommon to encounter spurious, unilateral tail molt, for on June 11, July 11, and July 12, birds were taken each of which was molting only one tail feather (not the lateral ones) whereas all of the other rectrices were old. The inception of tail molt was not determined precisely, but presumably it occurs in late July. Eleven adults obtained on July 12 and 13 showed no signs of tail molt. Even though most adults showed some indications of molt of the rectrices or primaries until early October, occasionally birds believed to be adults on the basis of skull ossification had completed their molt as early as September 19. After September 1, three out of eight adults had completed their molt, and on the basis of plumage alone they would have been indistinguishable from immatures.

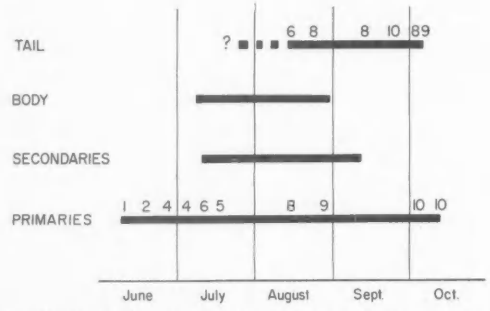

Fig. 1. Timing of the postnuptial molt of the adult Chimney Swift near Macon, Georgia. Numerals indicate the numbers of new feathers for a given area of the body on a specific day.

Molt data for immature birds are meager here because of the relatively small sample obtained, but there is evidence from ten birds that no significant amount of molt occurs in the immatures once they have left the nest. One immature, taken on July 14, had nearly all of its feathers (remiges, rectrices, body feathers) still partly ensheathed, and evidently it had not been out of the nest very long. Other immatures, taken from late July until early October, showed only slight traces of body molt with the exception of one bird which was molting a few upper and lower tail coverts.

From these data, then, it would seem that until about mid-September a molting bird is almost certainly an adult, but after this time the character of molt must be used with some caution.

Skull ossification.—Conventionally the degree of skull ossification has been used in some passerine species to distinguish immature from adult birds in the fall, and using this fact as a working hypothesis, I began to observe and draw the skull of each swift with the hope that this character might assist in distinguishing age groups. All of the birds examined, however, from April through October had incompletely ossified skulls. In fact, after having examined 75 swifts of all ages and sexes taken at all seasons, I have not yet found a swift with a completely ossified skull! This seems to indicate that skull ossification would be unreliable for determining age, but such was not entirely the case, for some birds taken in the fall (immatures on the basis of no molt) had larger unossified "windows" in the skull than did adults. By spring and early summer, however, the unossified "windows" of all birds were essentially of the same size so that it was impossible to distinguish one-year-olds from older birds on the basis of this character.

Figure 2 illustrates the degree of skull ossification of several individuals, showing how this character might be used relatively to distinguish birds-of-the-year from adults in the late summer and fall.

Bursa of Fabricius.—The bursa of each swift was not examined routinely, but in the few birds which were studied, this saccular structure was large in birds-of-the-year and absent in adults, both taken in mid-July. The bursa in one immature male, for example, was 9×4 mm. (outside measurement). It is perhaps true that this structure could be used to distinguish age groups in the fall, but further research is needed before it can be used accurately.

Gonadal studies.—As part of the routine examination of each swift, the seasonal

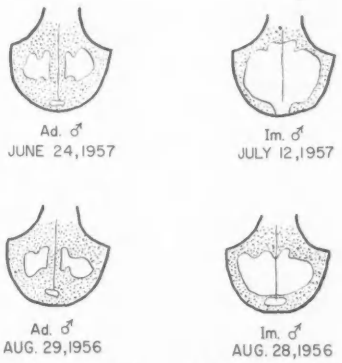

Fig. 2. Typical patterns of skull ossification in the Chimney Swift. Note the relatively smaller unossified "windows" in the adults.

activity of the gonad was checked as follows: In males the length and color of the left testis were recorded, and in females the largest follicle was measured. Of the birds which could be sexed and aged properly, measurements of gonads were obtained from 37 adult males, 5 immature males, 21 adult females, and 2 immature females. Ten other birds were examined for salivary glands, molt, and other characters, but their sex and/or age could not be determined accurately. Therefore, only 65 of the 75 Chimney Swifts are included in these gonadal studies.

Figure 3 shows testis and follicle size of adults plotted against the date. It is apparent from these data that the maximum testis size was reached in the latter part of May and early June, and that there was a regression of testis size beginning at about mid-June. By the first week in July testes had generally reached a minimum size of two or three millimeters, a size which was maintained at least until fall migration. Although the data are less complete for females, there was apparently a similar increase in gonadal activity at the end of May. The only female obtained which had significantly enlarged follicles was a bird taken on May 30, 1955. Its cloaca was open and expanded, and internally there was (1) a white egg with shell in the oviduct, (2) a 9-mm. yellow ovum in the body cavity next to the ovary, and (3) a follicle 4 mm. in diameter in the ovary. The nonbreeding follicle size was reached by early July at the latest, after which follicles were less than one millimeter.

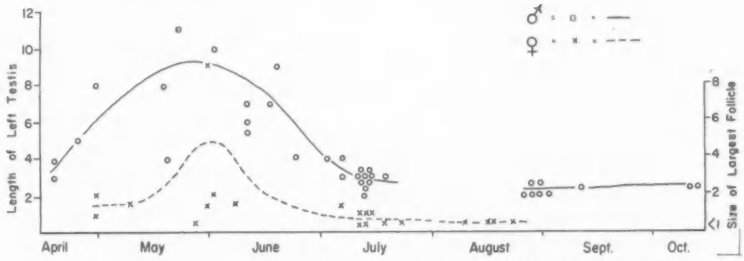

Fig. 3. Seasonal gonadal cycles in the Chimney Swift. Measurements are in millimeters.

Generally, however, the collecting of females at the height of breeding was unsuccessful. This might have been due to the fact that in feral birds there is a general tendency for a sudden recrudescence and regression of macroscopic ovarian activity. It is also possible that breeding female Chimney Swifts remain closer to the nests than do males, and therefore are less frequently encountered in random collecting. In the present study, for example, in the months of May and June, 11 males were taken whereas only six females were collected. These data at first might suggest a preponderance of males in the population, but an alternative hypothesis suggests that females are simply harder to obtain because of their duties at the nest. Fischer (MS) presents evidence in support of this suggestion since he found that the female does a little more than one-half of the incubating and later tends to cover the young more than the male does.

The five male birds-of-the-year were taken on July 12 and 13, August 28 and 29, and September 3. All of these had testes 1.5 to 2 mm. in length, sizes generally smaller than those of adults taken at the same time. The two female birds-of-the-year were taken on July 26 and August 23. Their follicles were less than one millimeter in diameter.

By careful scrutiny of figure 3, certain deviations become apparent. For example, a male taken on May 19 had a testis 4 mm. long, and a female taken on May 27 had almost indistinguishable follicles. Both of these measurements were obviously below the average sizes for adults at that season. Since the sample size was somewhat smaller than statistical treatment would normally require, one might explain these as deviations from the expected norm. However, even with our limited knowledge of the breeding biology of the Chimney Swift, an alternative explanation might be that these were nonbreeding, first-year birds, and that actually their measurements belong to a sample quite different from that of the adults. This proposition is further substantiated by the fact that the salivary glands of this male were small (3 mg.) and those of the female were equally undeveloped (6 mg.). It is of course possible that these were adults which would eventually breed, but because of the late date on which they were shot, this was probably not true. As far as the breeding of first-year swifts is concerned, Fischer (MS) states that the Alpine Swift (*Apus melba*) may breed in the first summer after hatching but that they do not usually breed until the second summer. In a marked population of the Chimney Swift, he found that five out of ten birds nested in the first summer after hatching.

One of the difficulties in working with these swifts at the latitude of central Georgia is the fact that birds taken in April and early May could be either migrants or resident birds. Furthermore, without a marked population it is impossible to know how long the birds collected in early spring had been at the given locality. The birds taken in April, for example, could have been in central Georgia for hours or for weeks. Even with these difficulties in mind, the suggestion is made here that early migrants have somewhat enlarged gonads (males with testes of 3 to 5 mm.). Further intensive collecting in late March might substantiate this point.

From the foregoing data on characters of age and sex, it becomes apparent that usually a thorough dissection is necessary before the sex and age of the Chimney Swift can be ascertained with accuracy. Molt in the fall is the best single external clue to age, but even it is not always reliable.

SALIVARY GLANDS

For many years it has been believed that swifts and swiftlets of several species use saliva in the construction of their nests, although an alternative hypothesis suggested (Home in 1817, *fide* Marshall and Folley, 1956) that gastric glandular secretions were used to bind nests together in at least one swiftlet. It has now been demonstrated conclusively by Marshall and Folley that only the secretions from the salivary glands are

used to any extent in nest construction by swiftlets. Histological studies showed an increase in the development of the salivary glands but no such increase in either the esophagus or proventriculus. In marshaling evidence for his revision of the genera of swifts, Lack (1956:2) stated that "all swifts use saliva for sticking together the materials of their nests, and all, so far as known, have enlarged salivary glands in both sexes in the breeding season." It seems to me that he generalizes too much by using the term "all," for the breeding habits of many swifts are incompletely known. Even a cursory survey of the literature will reveal the fact that some swifts use mud in the construction of their nest (for example, *Streptoprocne*) and, hence, *may* not use saliva. In fact, Ridgway (1911:703), writing about the Black Swift of western North America (*Nephoecetes* = *Cypseloides*), states that the nest is "loosely put together and not held together by salivary secretion." A similar observation was made by Legg (1956) on a sea-cave nest of the Black Swift. These observations do not preclude the possibility that these species in fact do have active or specialized salivary glands, but, until each species is examined anatomically, it is incorrect to say that *all* swifts have enlarged salivary glands in the breeding season and use saliva in construction of nests.

Elsewhere in the literature, one encounters other misleading and unsubstantiated statements regarding salivary glands. Certainly some other species of birds do have salivary glands, but they may not be well developed and may not be used in nest construction. Wing (1956:61) states that "other swifts [than *Collocalia*] use secretions of the salivary glands in cementing their nests together, as do Swallows also." Again, a cursory survey of the literature reveals no reference which proves that North American swallows use saliva as nest cement. Bent (1942:472) quotes Coues to the effect that Cliff Swallows (*Petrochelidon pyrrhonota*) probably do not use saliva but rather mud in nest construction, and in writing about the Barn Swallow (*Hirundo rustica*) he says (*op. cit.*: 445) that "Professor Herrick . . . feels confident that the bird's saliva is not a factor in making the mud more adhesive." Marshall and Folley (1956) could not find salivary glands in the Australian Welcome Swallow (*Hirundo neoxena*). It remains for further research to demonstrate whether or not these unrelated birds have salivary glands and if the saliva is used in nest construction.

Gross appearance.—The salivary glands of the Chimney Swift are paired structures located beneath the ventral oral epithelium. Since they occupy this position even in the most advanced seasonal state, it would seem best to refer to them as sublingual glands and not buccal (see later discussion). In the two species of *Collocalia* studied and illustrated by Marshall and Folley (*op. cit.*:385) the salivary glands are similar in appearance and position to those described for the Chimney Swift.

When observed in the undeveloped state (nonbreeding adults and birds-of-the-year), these glands are separated by a wide space in the midline; thus they lie to either side of the mid-ventral line just under the skin (see fig. 4*a*). In this condition each gland narrows to a point anteriorly in a series of "cords" or "strings," which disappear into the floor of the mouth. Each gland is approximately 7 mm. in length and 2 mm. in width at its widest point, which is most posterior. In this undeveloped state it was not possible to distinguish between the glands of adults and those of birds-of-the-year on the basis of gross appearance alone, but, as will be shown later, weight of the gland offers some clue to the age of the bird.

In the fully developed condition, that is, at or about the height of the breeding season, each gland swells considerably in three dimensions until it occupies completely the area between the floor of the mouth and the skin surface (see fig. 4*b*). Each becomes highly vascular and measures approximately 14 mm. long and 5 mm. wide.

It is of interest to note that, of the two species of *Collocalia* studied by Marshall

Fig. 4. *a*. Undeveloped salivary glands from adult female Chimney Swift taken on April 30, 1955, near Sandersville, Georgia; *b*. fully developed salivary glands from adult female Chimney Swift taken on May 30, 1956, at Macon, Georgia.

and Folley, taken from the same cave on the same day, one (*brevirostris*) was evidently breeding, as indicated by its enlarged salivary glands, whereas the other (*francica*) was not breeding because it had small glands. The illustrations given for these two species closely resemble the seasonal developmental picture given for the Chimney Swifts in figure 4.

Seasonal development.—The enlargement of the glands in three dimensions precludes the possibility of using any single linear measurement as a reliable index for size increase. Also, since the glands do not have a definite geometric shape, one cannot use a standard formula to compute volume as is frequently done in the routine presentation of testis recrudescence, where the volume of an ellipsoid can be used. It was decided, therefore, to dissect out one gland carefully; even in an advanced state of development a distinct separation could be made in the mid-line. The other gland was left *in situ* for later histologic study. These glands, having been stored in 70 per cent alcohol, were then dried carefully and thoroughly on a piece of filter paper, after which they were weighed on a Beckman Chainomatic balance to the nearest tenth of a milligram. Since there was some question of reliability at this level due to possible differential fluid infusion or a minute error in dissection, the figures were rounded off to milligrams. Routinely, then, the salivary glands were weighed in this fashion, with the exception of two or three which had been damaged by shot.

In figure 5, the weights of one of the salivary glands dissected from adults are plotted

against time of the year. As in the case of the gonads, some of these measurements might have been from nonbreeding and/or first-year birds. However, since these age groups could not be distinguished, all measurements are included in this graph with the exception of those of known birds-of-the-year.

Although there is a correlation between the retrogression of gonads and salivary glands, comparison of figure 3 on gonad development and figure 5 on salivary gland development indicates that the testes develop earlier than the salivary glands. For example, the testes of residents which have just arrived and/or migrants in late April are about one-half the maximum size to which they will develop later, but the salivary glands of these same birds are less than one-tenth the maximum size. Although the curve of developing gonads is a gradual one, the salivary glands seem to develop more abruptly. These anatomical facts being true, it is probable that the physiological mechanisms which trigger male gonadal development occur before those which result in the enlarged salivary glands. It is of further interest to note that the regression of salivary glands and of gonads is a gradual one and it is generally consummated by mid-July or slightly before.

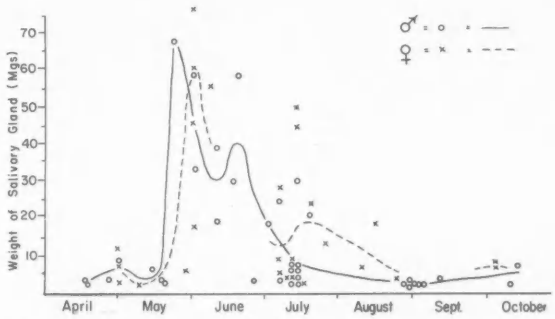

Fig. 5. Weight of one salivary gland from each bird, according to season and sex.

Figure 5 shows that the trends for salivary gland development in the two sexes are nearly identical. The bimodal trendline is probably spurious and results from inadequate sampling in June and July. The seasonal glandular development in both sexes is to be expected, for Fischer (MS) and other workers have shown that both sexes take apparently equal roles in nest construction. Also, Fischer points out that the saliva may be used throughout incubation. In fact, a semicircle of saliva is added to the wall above the nest after incubation begins; this reinforces the nest.

Histological appearance.—Serial sections were prepared of six salivary glands and the associated mouth epithelium, and representative sections of several other glands were examined for comparative purposes. These were cut at 10 microns and were stained with Harris' hematoxylin and eosin. Drawings of three glands are presented in figure 6, and these are intended to represent typical glands in the inactive, regressing, and active conditions.

The active gland was taken from an adult male, shot on May 22, with a near maximum weight of the salivary gland (68 mg.). In this condition it is evident that the stratified squamous epithelium and the buccal glands are larger than in the inactive gland. The cells of each salivary gland lobe were evidently principally mucous-secreting, but some serous cells might have been present although not in demilunes. These mucous cells

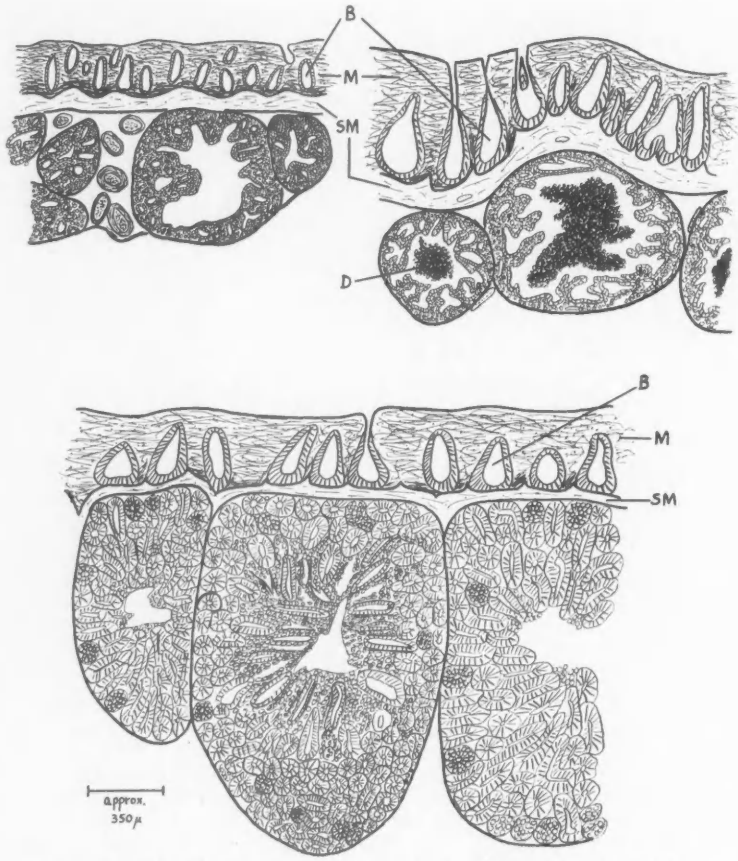

Fig. 6. Drawings of oral epithelium and lobes of salivary glands X 100. Upper left, inactive gland; upper right, regressing gland; lower, active gland. B—buccal gland; M—mucosa; SM—submucosa; D—detritus.

of the buccal and salivary glands were columnar in shape. The lumina of the salivary gland lobes did not appear to be lined with a cuboidal epithelium in the active condition, but in the inactive gland such an epithelium was noted. Serial sections showed that each of these lumina opened one by one toward the anterior part of the gland until each lobe had emptied its products into the oral cavity beneath and anterior to the tongue.

The salivary gland (39 mg.) from an adult male taken on June 11 was used to exemplify a regressing condition in figure 6. Whereas the mouth epithelium and buccal glands resemble those in the active condition, the lobes of the salivary glands are noticeably smaller. Histologically these lobes are irregular internally with only a few well developed tubules and alveoli, and in each large lumen there is a mass of cellular debris. Apparently this represents cells cast off from the tubules as the gland shrinks to an inactive condi-

tion and size. This phenomenon resembles a similar one observed in the regressing testes of many birds and mammals.

For the inactive state a gland weighing 3.2 mg. was chosen from an adult male, taken on August 29. As contrasted with the other two drawings in figure 6, the mouth epithelium, buccal glands, and lobes of the salivary glands are all smaller and presumably not secreting. Mucous cells of the glands are principally cuboidal in shape.

Hormonal and/or nervous control.—To date there are no experimental data which show conclusively the controlling mechanisms responsible for the growth and secretion of salivary glands in swifts, but recent experimental evidence from mammals bears upon this situation in birds. As Marshall and Folley (*op. cit.*:387) correctly averred, Lacassagne and other French workers (*fide* Shafer, Clark, and Muhler, 1956) have demonstrated in the rat and mouse relationships between various sex hormones and the submaxillary salivary glands. For some time it was believed that androgens alone were responsible for the maintenance of size and activity of these glands, but in the past 15 years additional research on other hormones has shown that it is not just a simple one-to-one relationship. Currently research in this field is being conducted because of the important relationship between saliva and dental caries in mammals.

In a recent publication, Shafer, Clark, and Muhler (*op. cit.*) have summarized the current knowledge relating to hypophysectomized rats and their salivary glands. Their findings indicate an intricate relationship among testosterone, thyroxine, and the anterior pituitary gland hormone(s). As the result of hypophysectomy the submaxillary glands of rats atrophy. Upon the simultaneous administration of both thyroxine and testosterone, it was found that atrophy of the glands could be inhibited, whereas other hormones (cortisone, pituitary growth hormone, insulin, estradiol, and progesterone) were largely ineffective in inhibiting the atrophy of the salivary glands.

Lacassagne (1940) demonstrated a sexual difference in the submaxillary gland of mice, and suggested that male saliva differs in quality from female saliva. In the present study on the salivary glands of the Chimney Swift, I was unable to find any sexual differences in these glands either macro- or microscopically, and since the existing life history data indicate that both sexes use saliva in the same fashion, one would expect *a priori* no sexual difference in the avian salivary glands.

Few if any concrete data are available concerning the nervous control of salivary gland development, but Grad and Leblond (*fide* Shafer and Muhler, 1955:148) "have pointed out the synergistic effect of testosterone and thyroxine on the rat submaxillary gland and state that because of this apparent major role of these hormones, nervous influences on this gland are of little significance."

Although it is usually unwise to make general statements about hormonal relationships in different animals, it seems reasonable here to suggest a tentative working hypothesis for a possible hormonal-anatomical mechanism in the swifts. These suggestions are, of course, based upon the foregoing experimental evidence from mammals. At the onset of breeding in the Chimney Swift, it can be stated that the titers for androgens and some anterior pituitary gland hormones are high. This is possibly also true for the thyroid hormone, but there is less supporting evidence. If these facts are true, then the combined action of these hormones could cause the growth and perhaps the secretory activity of the salivary glands. Nervous factors may play some role in this picture, especially at the point of secretion. This hypothesis could be tested experimentally by the removal of certain glands and the subsequent administration of the appropriate hormones if someone could devise a method of keeping swifts in a fairly natural state in captivity.

SUMMARY

Seventy-five Chimney Swifts were collected over a period of three years in Georgia and South Carolina in order to effect a study of their paired salivary glands. In the course of the study, data were assembled on molt, weight, skull ossification, and gonad size in an attempt to discover criteria for sex and age. With the possible exception of molt, dissection is necessary to determine sex and age.

Salivary glands were studied (1) by weighing one gland from each bird to the nearest milligram and (2) by preparing some histologic sections. Weights revealed seasonal enlargements similar to cyclical gonadal enlargement, as did the microscopic material. Sections also revealed enlargement of the oral epithelium and buccal glands.

It is tentatively suggested that the *modus operandi* for the enlargement and possible secretion of the glands is mediated via hormones, namely, the combined actions of testosterone, thyroxine, and hormone(s) from the pituitary gland.

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HYBRIDIZATION IN THE RED-EYED TOWHEES OF MEXICO: THE EASTERN PLATEAU POPULATIONS

By CHARLES G. SIBLEY and DAVID A. WEST

The occurrence and significance of hybridization is a matter of interest to investigators in many branches of biology. The role of hybridization as a factor in evolution has attracted special interest. Much of the pertinent literature concerns plant hybrids (cf. Anderson, 1949; Dobzhansky, 1951; Stebbins, 1950), but hybridization in animals is also receiving attention (cf. Mayr, 1942; Sibley, 1950, 1954, 1957; Miller, 1955). The papers just cited contain discussions of the theoretical background of the subject, especially as it relates to birds.

In the present paper we wish to present the results of a continuation of the studies reported upon in two previous papers by the senior author (1950, 1954).

ACKNOWLEDGMENTS

Our special thanks are expressed to the members of the field parties who collected the material. Additional support for the field work came from the New York State College of Agriculture and the Faculty Research Grants Fund of Cornell University. Dr. Walter T. Federer advised on the statistical aspects of the discussion. In addition to participating in the field work Walter J. Bock and Lester L. Short, Jr., have read the manuscript and have made many helpful suggestions.

MATERIALS

The present study is based primarily on a collection made in 1954 and not previously reported upon. In calculating the hybrid indexes, and other measurements of populations, the specimens described in the 1950 and 1954 papers have been included. Additional material was studied for the first time during the summer of 1954 in the collections of the British Museum (Natural History).

The 1954 collection of new material contains 338 adult specimens. These are deposited in the collection of Cornell University. The British Museum collections contain 90 specimens used in this study. Material previously reported upon from all parts of México (Sibley, 1954:254) totaled 1130 specimens. To the present time (1957) the study of Mexican towhee hybrids is based upon 1560 specimens. Approximately 1000 of these have been collected in the years 1946, 1948, 1950, and 1954 in the course of expeditions devoted to the study of this problem. The remainder are specimens contained in various collections in the United States and Europe (cf. Sibley, 1950).

THE ANALYSIS OF HYBRIDS

The "hybrid index" method was developed in the course of studies on plant hybrids (cf. Anderson, 1949) and has proved useful in the analysis of avian hybrids (Sibley, 1950; Dixon, 1955). It provides a rough quantitative evaluation of the complicated color patterns of hybrid individuals resulting from recombinations of the characters of unlike parental forms.

The two species of red-eyed towhees which hybridize in México are the Rufous-sided Towhee (= Spotted Towhee), *Pipilo erythrophthalmus*, and the Collared Towhee (*Pipilo ocai*). Detailed descriptions and a color plate are given in a previous paper (Sibley, 1950). For the convenience of those not having ready access to this paper the following synoptic descriptions are presented.

Pure populations of the two species differ in plumage color in six principal areas.

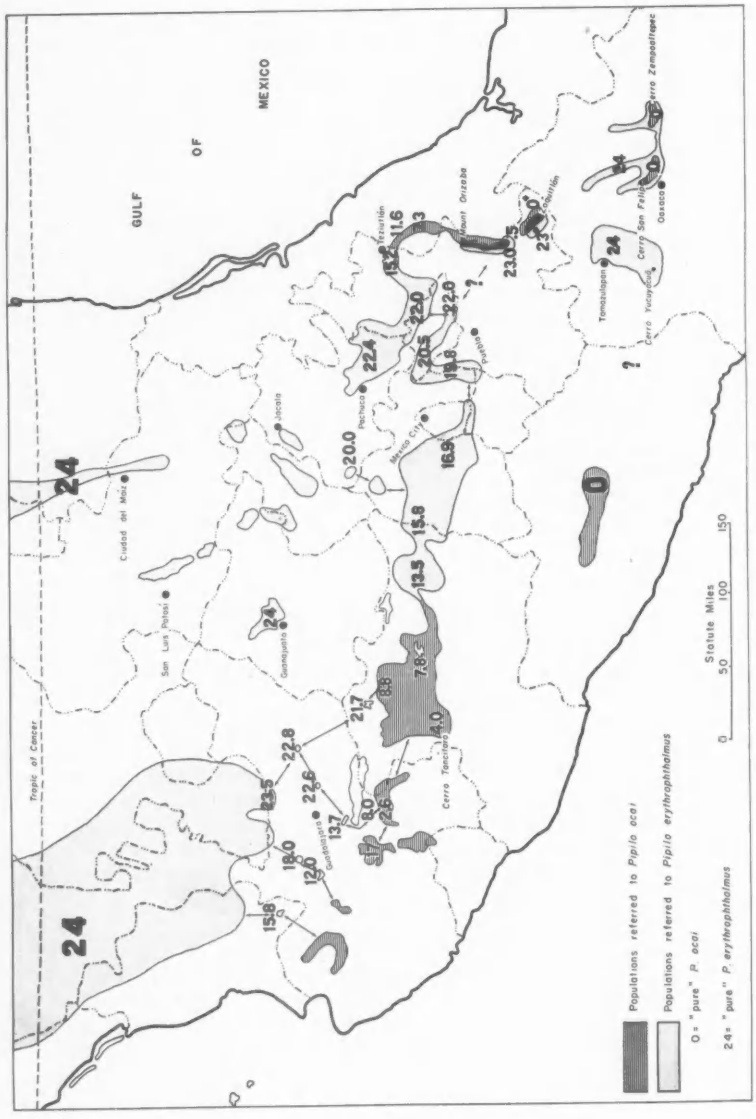

Fig. 1. Distribution of the red-eyed towhees in central México.

1. Pileum color: Chestnut in *ocai*, black in *erythrophthalmus*.
2. Back and wing spots: White spots on scapulars and wing coverts in *erythrophthalmus*. These areas are unspotted in *ocai*.
3. Back color: Green in *ocai*, black in *erythrophthalmus*.
4. Throat color: White in *ocai*, black in *erythrophthalmus*.
5. Flank color: Brownish olive in *ocai*, rufous in *erythrophthalmus*.
6. Tailspots: White spots on three outer rectrices in *erythrophthalmus*, absent in *ocai*.

For each of these six characters five gradations ranging from pure *ocai* to pure *erythrophthalmus* may be distinguished. These gradations are scored as follows:

"0" When expressed as in pure *P. ocai*.
"1" Mainly as in *ocai* but showing some influence from *erythrophthalmus*.
"2" Intermediate between *ocai* and *erythrophthalmus*.
"3" Mainly as in *erythrophthalmus* but showing some influence from *ocai*.
"4" When expressed as in pure *P. erythrophthalmus*.

A pure *ocai* specimen will thus be scored "0" for all six characters for a summated score of "0" ($6 \times 0 = 0$). A pure *erythrophthalmus* will score "4" for each of the six characters for a summated score of "24" ($6 \times 4 = 24$). Hybrid scores will fall on this "0" to "24" scale, a specimen with a score of "12" being at the midpoint, and so forth. Figure 1 indicates the average hybrid index numbers for the populations which have been sampled to date. Additions since the 1954 paper are mainly in the eastern plateau area.

MEASUREMENTS OF SIZE

The weights in grams of the 338 specimens collected in 1954 were obtained. The British Museum specimens had not been weighed. Linear measurements from skins, in millimeters, were taken as follows: wing, the chord; tail, from the insertion of the two middle rectrices; tarsus, from the joint between the tarsus and the tibia (the heel) to the midpoint of the distal margin of the most distal undivided scute; bill, from the anterior margin of the nostril to the tip of the maxilla.

SUMMARY OF PREVIOUS RESULTS

The map (fig. 1) indicates the distribution of the red-eyed towhees of México as presently known. The numbers are hybrid index averages for each population sample. The Rufous-sided Towhee (*P. erythrophthalmus*) is a widespread species which ranges from Canada to Guatemala. In México it is primarily restricted to brushy undergrowth between 5500 and 9000 feet elevation. In the Mexican plateau at these altitudes oaks (*Quercus*) tend to be the dominant trees. The Collared Towhee (*P. ocai*) is restricted geographically to the higher mountains of the Mexican plateau, usually above the altitudes occupied by *P. erythrophthalmus*. The Collared Towhee inhabits the dense undergrowth associated with coniferous (pine, fir) woodland and is thus in but limited contact with the Rufous-sided Towhee.

In the state of Oaxaca, in southeastern México, the two species occur side by side (Cerro San Felipe), but no evidence of interbreeding between them has been found. In the mountains which form the eastern edge of the Mexican plateau, between Zoquitlán and the Cofre de Perote, there are populations of both species, often occurring in sympatry. Hybrids occur in this area, but they tend to be infrequent. In the Teziutlán, Puebla area, a hybrid population is found in which all individuals are intermediate between the parental forms. Extending across the central highlands, from northeast of Mexico City to the mountains of southwestern Jalisco, is a clinal series of populations which gradually bridges the geographical and morphological gaps between nearly pure *erythrophthalmus* in Hidalgo (Pachuca) to nearly pure *ocai* in Jalisco. On isolated mountain tops in western México (Cerro Viejo, Cerro Grande, Cerro Gordo, Cerro El

Fig. 2. Localities in eastern México mentioned in the text.

Fraile, Cerro Tequila, Cerro El Faro, Sierra de Ameca, Cerro García) occur hybrid populations which show the effects of introgression. A population of pure *ocai* is found in the Sierra Madre del Sur of Guerrero, and pure *erythrophthalmas* ranges northward in the Sierra Madre Occidental and the Sierra Madre Oriental and southward in the mountains of Chiapas and Guatemala.

The field studies in Hidalgo, Puebla, Veracruz, and Oaxaca had shown that the pattern of variation in the eastern plateau was complex and required further attention. Prior to 1954 collections had been made, or specimens collected by others had been examined, from several localities. In the following list, our localities are numbered and the years in which they were visited are noted in parentheses. Figure 2 indicates the location of localities mentioned in the text.

Hidalgo: 6 mi. N Pachuca, 9600 ft. (1946). Other specimens examined from El Chico, Real del Monte, San Agustín, Irolo, Tulancingo, and Apulco. *Puebla:* 8 mi. NE Chalchicomula, 10,350 ft. (1946, 1948); 3 mi. W Teziutlán, 7300 ft. (1950); additional material examined from Honey, Beristain, Chalchicomula, Mount Orizaba, and Tochimilco. *Veracruz:* Puerto Morelos, 8000 ft., 19 mi. WSW Orizaba (1950); additional material from Las Vigas and Cofre de Perote. *Oaxaca:* La Cumbre, 5 mi. NE Cerro San Felipe, 9000 ft. (1946, 1948); other specimens from Cerro San Felipe, Mount Zempoaltepec, and mountains near Ozolotepec. From Tlaxcala only two specimens from Mount Malinche had been examined.

THE 1954 FIELD STUDY

Two field parties collected in the eastern highlands in June, July, and August. Party number 1, consisting of Walter J. Bock, Thomas Savage, and David B. Wingate, visited the following localities on the dates indicated. The number of adult towhee specimens from each locality is given in parentheses.

Cerro del Astillero, 9500 ft., 10 km. SSE Huichapan, Hidalgo, June 14–16, (53); Route 99, 9400 ft., at México-Tlaxcala border, 20 km. ENE Texcoco, México, June 19–23, (26); Las Mesas, 8700 ft., 13 km. WNW Apizaco, Tlaxcala, June 25–28, (17); Mount Malinche, 9400 ft., 17 km. SE Apizaco, Tlaxcala, June 29–July 1, (18); Tacopan, 13 km. W Teziutlán, 7400 ft., Puebla, July 3–6, (47); 20 km. N Perote, on Teziutlán-Perote highway, 7800 ft., Puebla, July 8–13, (23); Rancho Los Olmos, 8600 ft., 6 km. W Las Vigas, Veracruz, July 14–18, (18); Puerto Morelos, 8000 ft., 19 mi. WSW Orizaba, Veracruz, July 21–27, (73).

Party number 2, consisting of Lester L. Short, Jr., Fred C. Sibley, and Ralph H. Long, Jr., visited the following localities.

5 mi. NE Tlaxco, 9100 ft., Tlaxcala, August 1–5, (14); 10 mi. SE Mount Malinche, 8100 ft., Tlaxcala, August 9–10, (13); 4 mi. W Zoquitlán, 8400 ft., Puebla, August 11–17, (5); 2 mi. E Tlaxiaco, 5800 ft., Oaxaca, August 19–24, (10); La Cumbre, 9000 ft., 5 mi. NE Cerro San Felipe, Oaxaca, August 25–30, (21).

In the hybrid indexes and measurement tables the two localities on Mount Malinche are considered as one. The 73 specimens from Puerto Morelos are combined in this paper with 20 taken by Sibley (1954) in 1950 and the 47 from near Teziutlán with nine taken in 1950 plus two in the Chicago Natural History Museum.

THE DISTRIBUTION OF RED-EYED TOWHEES IN RELATION TO TOPOGRAPHY AND VEGETATION IN EASTERN MEXICO

The presently known distribution of red-eyed towhees in eastern México is indicated on the map, figure 1. As previously noted, *Pipilo erythrophthalmus* occurs mainly in the brushy understory associated with oak woodland, while *Pipilo ocai* occurs at higher elevations in the brush associated with pine-fir forest. In eastern México, neither species occurs below 5000 feet in the breeding season and most populations are found above 8000 feet. In addition to the direct effects of altitude on the vegetation, the "rain-shadow" effects of mountains have strongly influenced the distribution of vegetation

and hence the distribution of birds. Of principal importance is the semi-desert area to the west of Mount Orizaba resulting from the interception of moisture by the Mount Orizaba-Cofre de Perote chain. This has produced an arid region extending approximately from Tehuacán in the south to the section west of Perote in the north. Leopold (1950) includes this area in his "mesquite-grassland" formation. The northern part of this basin is a flat, open grassland extending from Zacatepec north to near the village of San Miguel, 27 miles by road north of Zacatepec. This grassland basin extends east and west for from 10 to 25 miles. South from Zacatepec to Tehuacán the rain-shadow of Mount Orizaba has produced an arid mesquite scrub area. As noted by Leopold, the principal plants include *Prosopis, Celtis, Fouquieria, Acacia,* many cacti, agave, and the pepper tree (*Schinus molle*), a non-native "escape." This arid belt, with its xerophytic habitats, is unsuitable for red-eyed towhees and constitutes an important barrier for these birds between the Mount Orizaba ranges and the uplands of Mount Malinche and other mountains west of the mesquite-grassland region.

To the south this barrier effect is continued by the arid valley in which the town of Tehuacán is situated. South of Tehuacán the valley continues to its connection with the Río Santo Domingo, a deep east-west chasm which bisects the mountains of the eastern edge of the plateau and flows eastward to enter the Río Papaloapan which drains to the Gulf of México. These valleys serve to isolate the Mount Orizaba highlands from the mountains of Oaxaca to the south and southwest. Further description of this area will be found in a previous paper (Sibley, 1954:277–279).

The rapid drop in elevation at the edge of the plateau is an effective barrier along the eastern and northern margin of the area under consideration. The highlands of the Popocatepetl-Ixtaccihuatl range communicate, via a low range of hills, with Mount Malinche (see fig. 1) and there appears to be no important discontinuity in towhee habitat between the uplands near Pachuca and the ranges running southeast toward Mount Malinche. South of Puebla the land slopes rapidly to the Río Balsas drainage system and the arid-tropical vegetation is unsuitable for towhees. More detailed information on topography, vegetation, and hybrid gradients follows.

Cerro del Astillero.—Cerro del Astillero (= C. Nopala) is located at 20° 18′N latitude and 99° 36′W longitude. It rises to 10,168 feet (World Aeronautical Chart, No. 589) from a semi-desert plateau of between 7000 and 8000 feet elevation. The xerophytic vegetation of the plateau is replaced at about 9200 feet by sparse oak woodland which continues to the summit. No pines are present. Towhees were first noted at 9000 feet and were one of the commonest bird species above 9500 feet.

The hybrid index of the 53 specimens ranges from "16" to "23" with an average of

Table 1

Measurements of Population from Cerro del Astillero

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	37	48.3±0.5	3.0	6.2
	♀	15	48.9±1.1	4.2	8.6
Wing	♂	38	88.6±0.4	2.1	2.4
	♀	15	83.4±0.6	2.4	2.9
Tail	♂	35	100.9±0.7	4.1	4.0
	♀	14	96.1±1.0	3.8	3.9
Tarsus	♂	36	29.9±0.2	0.9	2.9
	♀	15	28.7±0.3	1.0	3.4
Bill from nostril	♂	37	10.4±0.1	0.5	4.4
	♀	15	10.2±0.1	0.3	3.3

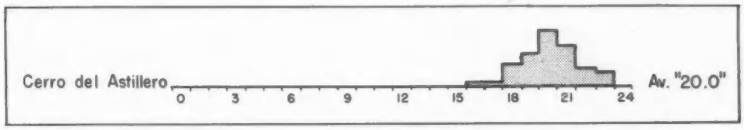

Fig. 3. Histogram of the hybrid indexes of specimens of red-eyed towhees from Cerro del Astillero, Hidalgo.

"20.0." Measurements are given in table 1 and the histogram of hybrid indexes in figure 3.

To the north and east of Cerro del Astillero the land is low and desert-like, providing a barrier to dispersal from the populations of *P. erythrophthalmus orientalis* > *maculatus* along the plateau edge north of Pachuca. To the southwest, high country extends toward eastern Michoacán. In 1950 the senior author drove north from Toluca to Querétaro. Along this route suitable towhee habitat apparently exists on Cerro Pelón de Nado, on Cerro Jocotitlan, and on all the land in this area over 9000 feet. The situation to the southeast of Cerro del Astillero is not clear, but it appears that the population of Cerro del Astillero is in closest contact with the populations to the south which form the "trans-plateau gradient" (Sibley, 1950:169–176).

20 km. ENE Texcoco.—This locality is on the highway (Route 99) which runs northeast from Texcoco, México, to Capulalpan, Tlaxcala. The actual collecting area was very near the Tlaxcala border in the state of México. The dominant trees are pines which extend to the summit at 10,500 feet. A few oaks are present and the higher slopes are covered with thick brush, including *Rhododendron*. Towhees were found in the brush above 9600 feet, but they were not abundant.

The hybrid index of the 26 specimens ranges from "16" to "24" with an average of "20.6." See table 2 for measurements and figure 4 for the histograms of hybrid indexes for this and the following localities. Figure 5 indicates the weights for the populations which were studied.

Table 2

Measurements of Population from 20 km. ENE of Texcoco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	20	50.9±0.6	2.7	5.3
	♀	6	46.7±1.3	3.3	7.0
Wing	♂	20	89.2±0.4	1.8	2.0
	♀	6	85.5±1.5	3.8	4.4
Tail	♂	19	105.9±0.8	3.6	3.4
	♀	6	101.2±2.8	6.9	6.9
Tarsus	♂	20	30.6±0.2	1.0	3.1
	♀	6	28.6±0.6	1.4	4.7
Bill from nostril	♂	20	10.4±0.1	0.1	1.0
	♀	6	10.0±0.2	0.4	4.5

This locality is situated at the northern end of the Popocatepetl-Ixtaccihuatl highlands. To the north and west the country is low and unsuitable for towhees. To the east low ridges extend to Mount Malinche providing suitable towhee habitat. The next locality lies in this area.

Las Mesas.—This locality is 32 miles east of the one described above. It too is on Route 99, at 8700 feet, in a pine-oak woodland where the conifers are dominant. The

land is badly eroded and there is little brush. Towhees, although not common, were found throughout the area. The 17 specimens have an average hybrid index of "20.5," ranging from "18" to "23."

Table 3

Measurements of Population from Las Mesas

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	47.9±0.9	3.2	6.6
	♀	5	46.3±1.0	2.3	5.0
Wing	♂	12	86.9±0.7	2.4	2.7
	♀	5	81.2±0.4	1.5	1.8
Tail	♂	12	100.0±1.2	4.1	4.1
	♀	5	94.7±0.8	2.9	3.0
Tarsus	♂	12	30.2±0.1	1.2	4.0
	♀	5	29.3±0.1	0.8	2.5
Bill from nostril	♂	11	10.2±0.2	0.6	5.5
	♀	4	10.3±0.1	0.1	1.4

Las Mesas is at the northern edge of suitable towhee habitat in this area. To the southeast, patches of suitable habitat provide a dispersal pathway to Mount Malinche.

Mount Malinche.—Both field parties worked on the slopes of Mount Malinche. Party number 1 collected on the northwest side of the peak from a camp at 9400 feet. Below 9700 feet, the land is cultivated and open, with brush restricted to the ravines and hedgerows. Pines are dominant from 10,000 to 13,300 feet, and above that point to the summit at 14,636 feet the peak is treeless. Towhees were found mainly in the hedgerows between cornfields from approximately 9000 to 10,000 feet. Very few were found in the pine forest, and the population was considered sparse by the collectors. Northward from Mount Malinche hedgerows, suitable for dispersal but probably not for breeding, extend across the lower country toward the Tlaxco region, approximately 25 miles north of Malinche. From the highlands near Tlaxco, there seems to be uninterrupted towhee habitat extending northwest to near Pachuca and, probably, around to the east to Teziutlán.

Party number 2 investigated the eastern and southeastern slopes of Mount Malinche. The eastern slope is similar to the northwestern side, as described previously. To the southeast, between the main mass of Malinche and a large parasitic cone near its base, the slope is gentler and scrub oaks, madrones, and brushy cover are more abundant. In this habitat towhees were fairly common.

Table 4

Measurements of Population from Mount Malinche

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	24	46.2±0.6	3.0	6.4
	♀	7	46.6±0.9	2.3	4.9
Wing	♂	24	87.8±0.8	3.8	4.3
	♀	7	80.4±0.7	1.8	2.2
Tail	♂	24	100.8±0.8	3.7	3.6
	♀	3	94.2		
Tarsus	♂	24	29.3±0.6	0.9	3.1
	♀	7	28.6±0.2	0.6	2.0
Bill from nostril	♂	24	10.1±0.1	0.5	4.8
	♀	7	10.0±0.2	0.5	5.4

The two parties collected a total of 31 specimens on Mount Malinche. These are considered together in all calculations. The hybrid index ranges from "20" to "24" with an average of "22.0."

Tlaxco.—The Tlaxco area, 25 miles north of Mount Malinche, is in the highlands which connect directly with the Pachuca region. At 9100 feet, 5 miles northeast of Tlaxco, pine forest, with thick undergrowth, is the dominant vegetation. Towhees were abundant and the 14 specimens have an average hybrid index of "22.0," ranging from "20" to "23." Specimens from Pachuca approximate this figure ("22.4"), and it is the same as for the Mount Malinche population. These figures indicate that gene flow from Pachuca to Malinche is relatively unimpeded. Measurements are given in table 5.

Table 5

Measurements of Population from Tlaxco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	6	48.9±1.1	2.7	5.5
	♀	5	49.8±1.7	3.7	7.4
Wing	♂	9	87.9±0.1	0.4	0.4
	♀	5	82.3±1.6	2.5	3.1
Tail	♂	9	101.4±0.2	2.2	2.1
	♀	5	97.6±2.2	4.8	4.9
Tarsus	♂	9	30.1±0.2	0.5	1.7
	♀	5	28.5±0.2	0.4	1.4
Bill from nostril	♂	9	10.2±0.2	0.5	4.6
	♀	5	9.9±0.2	0.5	4.8

Teziutlán.—This area was visited briefly in 1950 (Sibley, 1954:277) and 11 specimens were taken of which nine were adults. Two specimens from the collection of the Chicago Natural History Museum were also studied.

Party number 1 collected at Tacopan, 13 kilometers west of Teziutlán at 7400 feet. Towhees were common in the brushy undergrowth of pine-oak woodland, and 47 specimens were taken. Including the 11 adults reported on in 1954, a total of 58 specimens is now available. Of these 55 could be indexed and these range from "9" to "21" with an average hybrid index of "15.2." Measurements are given in table 6.

Table 6

Measurements of Population from Teziutlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	32	47.3±0.4	2.6	5.5
	♀	15	45.2±1.1	4.2	9.3
Wing	♂	34	82.6±0.4	2.4	2.9
	♀	20	78.8±1.4	2.0	2.5
Tail	♂	24	95.2±0.7	3.4	3.6
	♀	16	92.7±1.0	3.8	4.1
Tarsus	♂	35	29.9±0.2	1.1	3.7
	♀	20	28.6±0.2	0.9	3.1
Bill from nostril	♂	35	10.3±0.1	0.4	4.4
	♀	20	9.9±0.1	0.4	4.2

The Teziutlán hybrid population occupies a small basin of pine-oak woodland lying between the edge of the plateau to the east and a low range of hills to the west, beyond which the arid grasslands previously described constitute a barrier. Towhees extend at least to Zaragoza, 12 airline miles west of Teziutlán, and to Rancho San Miguel (Vera-

cruz), eight airline miles northeast of Teziutlán (= Km. 347, on the road to Nautla). To the southeast, toward Las Vigas, a narrow band of suitable habitat extends along the edge of the plateau between 6000 and 8000 feet elevation. This provides a slender, but seemingly unbroken, connection between the Teziutlán basin and the Cofre de Perote-Mount Orizaba region.

20 km. N Perote.—This locality is near the edge of the plateau at 7800 feet, approximately 13 miles southeast of Teziutlán and 12 miles north of Perote. The land is cultivated, but dense brush occurs in ravines. Pines are present, but with little undergrowth, and towhees are not common.

Table 7

Measurements of Population from 20 km. N of Perote

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	49.1±0.8	2.9	5.9
	♀	12	46.8±0.6	2.0	4.3
Wing	♂	12	83.3±0.5	1.7	2.0
	♀	12	78.2±0.8	2.6	3.3
Tail	♂	12	96.6±1.0	3.4	3.5
	♀	5	90.5±1.1	2.5	2.7
Tarsus	♂	12	29.7±0.2	0.2	0.7
	♀	12	28.8±0.2	0.6	2.1
Bill from nostril	♂	12	10.3±0.2	0.5	5.1
	♀	11	10.1±0.1	0.5	4.7

The 23 specimens range from "6" to "18" with an average hybrid index of "11.6." Table 7 contains data on measurements.

6 km. W Las Vigas.—This locality is approximately 10 miles southeast of the one previously described. The pine-oak woodland is dense and the undergrowth is thick. Towhees were found near 8600 feet but were not common. The 18 specimens collected in 1954, plus two in the British Museum (N.H.) from Las Vigas taken in 1888, range from "3" to "12" with an average index of "7.3." See table 8 for measurements.

Table 8

Measurements of Population from 6 km. W of Las Vigas

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	12	54.0±0.6	2.2	4.1
	♀	6	49.9±1.5	3.8	7.5
Wing	♂	12	84.1±0.8	2.7	3.2
	♀	6	79.2±0.8	2.0	2.6
Tail	♂	11	97.0±1.0	3.2	3.3
	♀	6	92.0±1.6	4.0	4.3
Tarsus	♂	12	31.1±0.2	0.7	2.2
	♀	6	29.4±0.5	1.1	3.8
Bill from nostril	♂	12	10.4±0.2	0.5	4.9
	♀	6	10.3±0.2	0.4	3.6

The shift in average hybrid index from the Teziutlán area ("15.2") to Las Vigas ("7.3") is extremely rapid. Over this distance of 23 airline miles the shift is 7.9 hybrid index units or .34 units per mile. This change is not as rapid as that between Cerro El Fraile and Las Joyas, Michoacán (.614/mile) but it compares closely with the shift between Cerro Grande and Cerro Viejo (.32/mile) and between Cerro Viejo and Cerro García, Jalisco (.33/mile) as previously reported (Sibley, 1954:264–273).

The El Fraile-Las Joyas shift is apparently the result of the vastly different ecological situations prevailing at these two localities which are 21 miles apart. The Cerro

Grande-Cerro Viejo and Cerro Viejo-Cerro García shifts reflect the influence of large gene pools at each end of the gradient on the small mountain-top populations. The rapid shift in the Teziutlán-Las Vigas area is due, seemingly, to this same effect. Introgression from the large *erythrophthalmus* populations between Pachuca ("22.4") and the Malinche area ("22.0") impinges upon the Teziutlán-Las Vigas gradient from one side while the Cofre de Perote *ocai* population exerts its influence from the other. The intervening populations, especially those between Teziutlán and Las Vigas, are small. Two specimens in the British Museum (N.H.), collected on the Cofre de Perote in 1889, have hybrid indexes of "2" and "3."

Cofre de Perote-Mount Orizaba.—The Cofre de Perote rises to more than 14,000 feet approximately 10 miles south of Las Vigas. The elevation drops to approximately 8000 feet at the south base of the Cofre, 20 miles south of Las Vigas, then rises rapidly southward to the summit of Mount Orizaba, 18,696 feet. The summit of Mount Orizaba is 43 miles south-southwest of Las Vigas and 13 miles north-northeast of Chalchicomula (= Ciudád Serdán). Twenty-four miles south of the summit, at Puerto Morelos, the altitude is 8000 feet.

The forest has been cleared on the western slope of Mount Orizaba up to approximately 10,000 feet. Originally these levels were covered with pines and oaks. Brush and small trees now occur in the ravines and on uncultivated areas. Between 10,000 and 10,500 feet, firs and alders are mixed with pine-oak woodland. A shrubby undergrowth of *Baccharis, Lupinus,* and other shrubs provides towhee habitat.

The occurrence of towhees in this region is complex. Both species are present, *erythrophthalmus* from approximately 8000 to 10,500 feet, *ocai* from 10,000 to at least 11,000 feet. Both are common in the overlap zone and occasional hybrids have been collected. Of 117 specimens, representing both species, 19 show evidence of hybridization (Sibley, 1950:162). As indicated in figure 4, a similar low incidence of hybridization is also present at Puerto Morelos and, so far as is known, at Zoquitlán. The *ocai* population of the Mount Orizaba area is in genetic contact with the Cofre de Perote population and on through the Teziutlán region to the *erythrophthalmus* populations of the Tlaxco-Pachuca area. The *erythrophthalmus* population of the Mount Orizaba-Puerto Morelos section apparently does not extend north much beyond Chalchicomula but just where it stops is not known. No specimens of *erythrophthalmus* are known from the Cofre de Perote. Another unknown factor is the amount of contact between the Mount Orizaba populations and that of Mount Malinche. Between Malinche and Orizaba there is a range of low hills, sparsely vegetated with oaks, junipers, and various xerophytes. This does not appear to be highly favorable for towhees but may permit some dispersal between Malinche and Orizaba. On the map (fig. 1) this connection is indicated by a "?" and arrows. Further work in this area is required to assess its influence.

Puerto Morelos.—Twenty-four miles south of the summit of Mount Orizaba, at 8000 feet, the road from Tehuacán, Puebla, to Orizaba, Veracruz, passes through this small village which is located at the highest point of the pass. The steep drop down the Cumbres de Acultzingo begins just east of Puerto Morelos. Oak woodland with *Baccharis* brush on the hillsides is the principal native vegetation. Pines occur in part of the area.

This locality was first visited in 1949 by R. J. Newman (Lowery and Dalquest, 1951:642–643) who collected one specimen each of *ocai* and *erythrophthalmus*. Neither showed evidence of hybridization but were found only 100 feet apart. In 1950, 13 specimens of *erythrophthalmus* and seven of *ocai* were obtained. Complete sympatry was established and evidence of hybridization was found (Sibley, 1954:277–278).

In 1954, party number 1 collected 53 *erythrophthalmus* and 20 *ocai,* providing a total from this locality of 67 *erythrophthalmus* and 28 *ocai.*

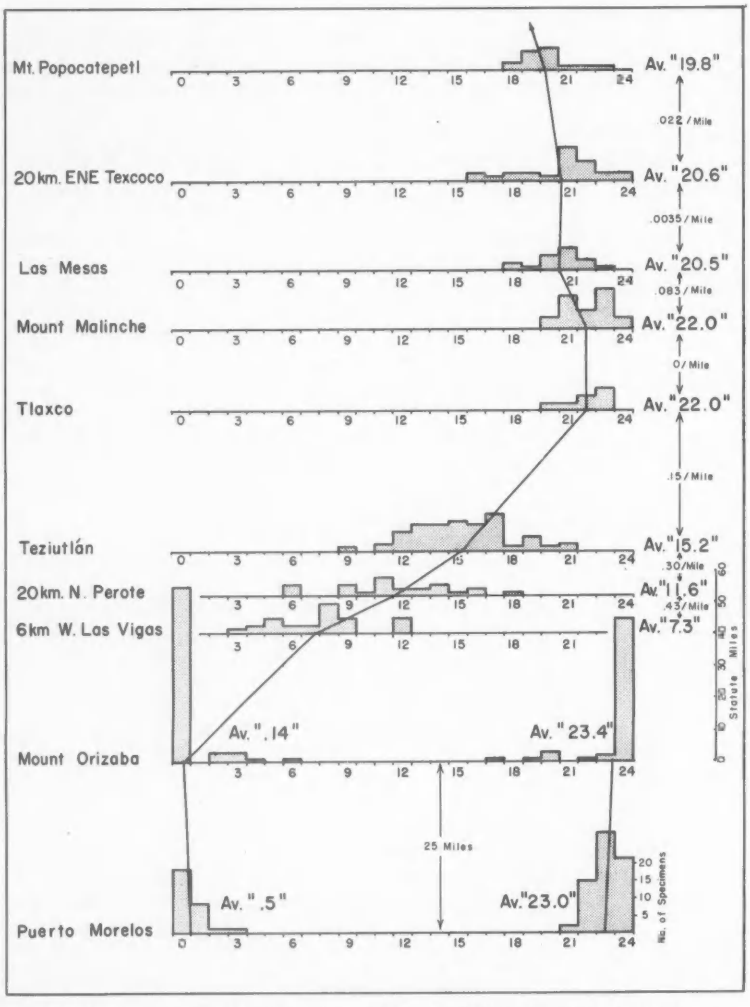

Fig. 4. Histograms of some hybrid populations in eastern México. Average hybrid indexes are connected by the line between samples. The shift in hybrid index units per air line mile is indicated. Except for the bottom sample the distances between base lines are proportional to actual air line distances between populations.

The *erythrophthalmus* range from "21" to "24" with an average hybrid index of "23.0." The *ocai* range from "0" to "3," averaging "0.5." The situation at Puerto Morelos is thus virtually identical to that on the west slope of Mount Orizaba. See tables 9 and 10 for measurements.

Zoquitlán.—In 1950 three specimens from "Zoquitlán, Puebla" in the collection of

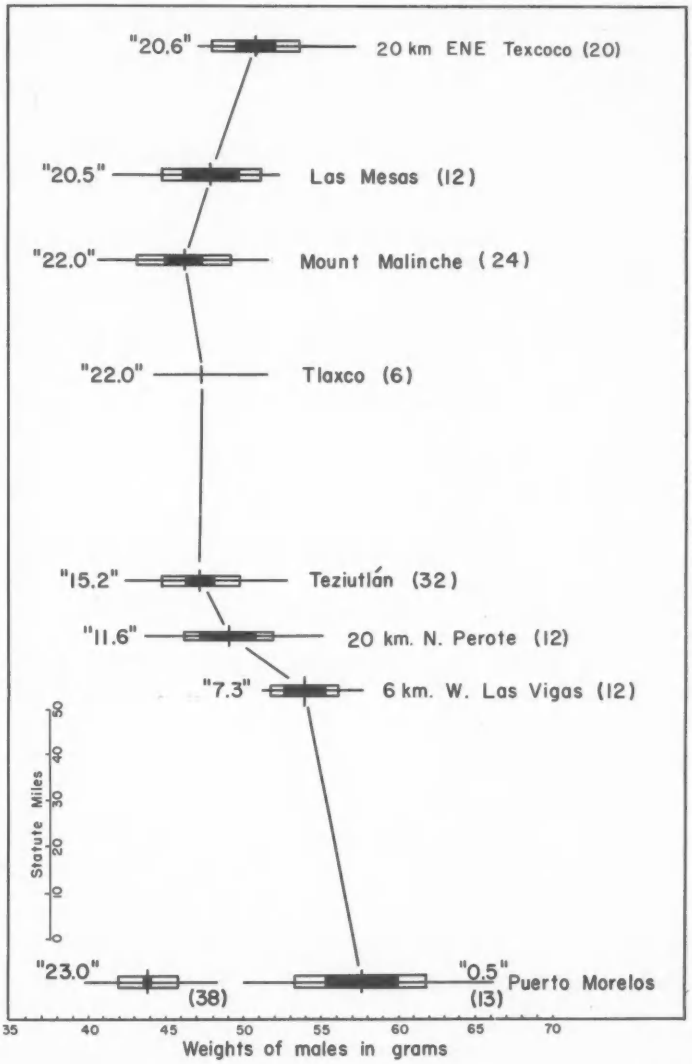

Fig. 5. Statistical analysis of weights of hybrid male red-eyed towhees from eastern México. Numbers in quotes are average hybrid indexes based on color; numbers in parentheses indicate number of specimens in the sample. Horizontal lines represent range; open rectangles indicate one standard deviation; solid black rectangles indicate twice the standard error of the mean; means are indicated by a vertical line; distance between samples is proportional to actual air line distance between populations; the angles formed by the lines connecting the means are proportional to the shift in weight between populations.

Table 9
Measurements of Population of *Pipilo erythrophthalmus* from Puerto Morelos

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	38	43.9±0.1	1.9	4.4
	♀	15	43.1±1.0	3.7	8.6
Wing	♂	44	83.3±0.3	2.0	2.1
	♀	20	78.9±0.4	1.6	2.0
Tail	♂	33	97.2±0.4	2.4	2.5
	♀	15	92.2±0.7	2.7	2.9
Tarsus	♂	43	28.4±0.2	1.0	3.5
	♀	20	27.6±0.4	1.8	6.5
Bill from nostril	♂	42	10.0±0.1	0.4	4.5
	♀	20	10.1±0.1	0.2	2.2

Table 10
Measurements of Population of *Pipilo ocai* from Puerto Morelos

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	13	57.7±1.1	4.1	7.1
	♀	7	56.1±1.9	5.0	8.9
Wing	♂	14	85.2±0.5	1.9	2.2
	♀	10	80.6±0.8	2.4	2.9
Tail	♂	13	98.9±1.1	3.9	4.0
	♀	4	92.3		
Tarsus	♂	14	30.8±0.2	0.9	3.0
	♀	10	30.8±0.5	1.5	4.9
Bill from nostril	♂	14	10.7±0.1	0.2	1.4
	♀	10	10.8±0.1	0.3	3.0

the Museo Nacional de la Historia Natural in Mexico City were examined (Sibley, 1954:278–279). One was a pure *ocai*, one a pure *erythrophthalmus*, and the third a hybrid with a summated index of "15."

Party number 2 collected at this locality, 35 miles southeast of Puerto Morelos, in August, 1954. The ridge forming the edge of the plateau reaches 9000 feet in altitude a short distance west of the town of Zoquitlán. To the east the slope drops rapidly through cloud forest to the lowlands of Veracruz. The western slope is drier and drops away to the arid valley south of Tehuacán. Near the summit of the ridge, pine-oak woodland, interspersed with cornfields, is the dominant vegetation. In this area, between 8000 and 9000 feet, the two species of towhees occur in sympatry, but neither seemed abundant. One specimen of *ocai* ("0") and four of *erythrophthalmus* were collected. The latter average "23.0," one being "22," two "23," and one "24." See tables 11 and 12 for measurements.

These specimens suggest that the situation at Zoquitlán is similar to that at Puerto Morelos and on Mount Orizaba, but additional material is needed from this area. In twenty-five miles, south of Zoquitlán, the land descends to 4000 feet in the valley of the Río Santo Domingo. As previously noted this valley, with its tributaries, isolates the Mount Orizaba-Zoquitlán highlands from the mountains to the south and west in Oaxaca.

Cerro San Felipe.—Collections have been made near the village of La Cumbre at 9000 feet, five miles northeast of the summit of Cerro San Felipe, in 1946, 1948 (Sibley, 1950:151–155), and 1954 when party number 2 obtained four *erythrophthalmus* and 17 *ocai*. To date a total of 31 adult *P. e. oaxacae* and 65 adult *P. o. brunnescens* have

Table 11

Measurements of Population of *Pipilo erythrophthalmus* from Zoquitlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	3	43.6		
	♀	1	(40.0)		
Wing	♂	3	80.9		
	♀	1	(79.0)		
Tail	♂	2	97.8		
	♀	1	(92.6)		
Tarsus	♂	3	28.2		
	♀	1	(28.1)		
Bill from nostril	♂	3	9.6		
	♀	1	(10.0)		

Table 12

Measurements of Population of *Pipilo ocai* from Zoquitlán

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	1	(62.8)		
	♀				
Wing	♂	1	(87.2)		
	♀				
Tail	♂	1	(102.5)		
	♀				
Tarsus	♂	1	(30.7)		
	♀				
Bill from nostril	♂	1	(11.4)		
	♀				

been examined from the highlands of Oaxaca; most of them have come from the Cerro San Felipe region. No convincing evidence of hybridization has, as yet, been detected.

At La Cumbre the two species are sympatric and abundant. As noted in the 1950 paper (Sibley, *op. cit.*:155), "these two forms react as good species in Oaxaca."

Although the absence of evidence of hybridization in this sample of 96 specimens does not prove that occasional hybrids are not produced, it does indicate that the incidence is less than at Puerto Morelos or on the west slope of Mount Orizaba. From Puerto Morelos the sample size (95) is the same, but of these at least 44 show some indication of introgression. Measurements are given in tables 13 and 14.

Table 13

Measurements of Population of *Pipilo erythrophthalmus* from Cerro San Felipe

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	14	42.9±0.2	2.7	6.2
	♀	10	40.5±0.6	1.8	4.4
Wing	♂	16	84.4±0.5	1.9	2.2
	♀	12	80.6±0.7	2.4	2.9
Tail	♂	15	95.4±0.6	2.4	2.5
	♀	12	92.0±0.9	3.0	3.3
Tarsus	♂	16	28.4±0.2	0.8	2.8
	♀	12	28.0±0.2	0.7	2.4
Bill from nostril	♂	16	10.1±0.3	0.1	1.1
	♀	12	9.9±0.1	0.4	3.8

Table 14

Measurements of Population of *Pipilo ocai* from Cerro San Felipe

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	31	61.3±0.6	3.4	5.5
	♀	22	58.5±0.8	3.8	6.5
Wing	♂	33	88.0±0.4	2.1	2.4
	♀	23	83.9±0.4	1.8	2.1
Tail	♂	32	105.1±0.7	3.8	3.6
	♀	20	98.8±0.8	3.4	3.4
Tarsus	♂	33	31.5±0.2	1.1	3.5
	♀	24	30.1±0.2	1.1	3.6
Bill from nostril	♂	33	11.5±0.1	0.6	5.4
	♀	23	11.2±0.1	0.5	4.6

Tlaxiaco.—Sixty-five miles west of Cerro San Felipe is the peak of Cerro Yucuyacua, rising to 11,074 feet. Party number 2 collected at 5800 feet near the town of Tlaxiaco which is on the north slope of Cerro Yucuyacua. The 10 specimens obtained may all be scored as "24" but, in some, there are suggestions of *ocai* influence which, if other specimens showing strong evidence of hybridization were also present, would logically be attributed to local introgressive effects. These include small amounts of white in the throats of four specimens, chestnut shaft streaks in the crown feathers of one, and some clouding of the tail spots of one. Similar variations occur in populations of *erythrophthalmus* in the United States, many hundreds of miles from the nearest *ocai* population.

Table 15

Measurements of Population from Tlaxiaco

Item	Sex	Number of specimens	Mean with standard error	Standard deviation	Coefficient of variation
Weight	♂	9	43.5±0.7	2.3	5.2
	♀	1	(42.6)		
Wing	♂	9	85.0±0.8	2.5	2.9
	♀	1	(80.3)		
Tail	♂	8	98.9±1.0	2.8	2.8
	♀	1	(93.9)		
Tarsus	♂	9	28.6±0.3	1.0	3.4
	♀	1	(29.3)		
Bill from nostril	♂	9	10.2±0.1	0.3	2.7
	♀	1	(11.0)		

For the present, therefore, it seems best to consider that these individuals represent "pure" examples of *erythrophthalmus*, but the area near Tlaxiaco, and west toward the Sierra Madre del Sur of Guerrero, should be more thoroughly explored. It is possible that a population of *ocai* occurs on the higher parts of Cerro Yucuyacua. Measurements are given in table 15.

The area near Tlaxiaco is covered with pine-oak woodland where it is not under cultivation. A similar forest seems to be present to the summit of Cerro Yucuyacua.

DISCUSSION

The information in this paper functions mainly to fill in detail and to add substance to speculations made in previous publications. Inevitably some new questions have been raised by this study. Since the beginning of this investigation in 1946, the situation in the Mount Orizaba-Puerto Morelos area has been recognized as of special interest. The

picture, as outlined in the present paper, is now much clearer than it was 11 years ago, but we are now even more convinced that this area deserves further detailed study. The principal question to be answered is this: Why should there be a seemingly unimpeded introgressive gradient from *erythrophthalmus* in the Pachuca area through the Teziutlán hybrids to the *ocai* on Mount Orizaba while these latter birds can exist in sympatry with another *erythrophthalmus* population with but little hybridization? In other words, why have the two species on Mount Orizaba and at Puerto Morelos not formed a hybrid population similar to the one at Teziutlán?

A second question relates to the situation in the mountains of western Oaxaca (for example, Cerro Yucuyacua) and eastern Guerrero. So little is known of this area that the present question must be restricted to a recognition of the need for exploration of the region between Cerro San Felipe, Oaxaca, and the mountains east of Chilpancingo, Guerrero.

The sympatric situation on Cerro San Felipe, Oaxaca, remains unchanged by the material collected in 1954. There is still no evidence of hybridization and no indication that appreciable dispersal occurs across the Río Santo Domingo barrier (see Sibley, 1954:287). We remain convinced that the patterns of variation observed in the Mexican red-eyed towhees are the result of hybridization and introgression.

In a recent paper (Sibley, 1957) the results of hybridization in birds have been considered in some detail. There is considerable evidence that hybridization is occasionally an important evolutionary factor and that the ultimate effects depend largely upon the direction of natural selection upon the hybrid genotypes. If the hybrids are not at a selective disadvantage, in comparison with the pure parental populations, the result will be introgression leading to swamping of the differences between the parental forms. Following a period of increased variability a new adaptive peak will become established, the variability will decrease to a "normal" amount, and a single, freely interbreeding population will have been re-established.

On the other hand, if the hybrids are selected against, they function as a source of selection against the individuals of both parental species which enter into mixed pairs. Any mechanism which reduces the incidence of mixed pairs is thus selected for with the result that, as long as the interaction continues, the isolating mechanisms of the parental species are reinforced relative to one another. Actual hybridization is not required to achieve "reinforcement" of isolating mechanisms or of characters which respond to interspecific competition. Any interaction between species which results in deleterious competition or the wastage of gametes will act as a source of selection tending to reduce that competition. It is apparently this source of selection which has brought about the diversity in species specific characters in sympatric species.

In the Mexican towhees, we may be observing several levels of these processes. So far as we can determine there is no evidence that selection is operating against the hybrids in the Teziutlán population or in the hybrid populations in Jalisco and Michoacán (Sibley, 1954). In these areas swamping may be in progress. The situation in the Mount Orizaba-Puerto Morelos section, where there is a low incidence of hybridization although both species are abundant and sympatric, suggests that selection in this area may be against the hybrids and that reinforcement is in progress. We do not necessarily favor this explanation and present it only as a possibility. It is difficult to believe that selection against hybrids could be reinforcing the isolating mechanisms of the Mount Orizaba birds faster than introgression from the Teziutlán population is breaking them down. We prefer to await further study of this situation before proposing an explanation of this problem.

The above remarks also serve to introduce our comments concerning the suggestion

by Brown and Wilson (1956:61–62) that "character displacement" may account for the characteristics of the hybrid populations of Mexican towhees. By "character displacement" these authors mean the same thing we have called "reinforcement." We might reconcile these two terms by the statement that the process of reinforcement results in character displacement (see Brown and Wilson, *op. cit.*:59). In other words, interspecific responses, when selected against, result in the reinforcement of characters which will act to reduce competition, gamete wastage, and the like. Brown and Wilson agree with this but favor the term "character displacement" when taxonomic characters are involved.

Although we agree (Sibley, 1957) with the interpretation of Brown and Wilson concerning the situation in the rock nuthatches (*Sitta neumayer* and *S. tephronota*) of Iran, we do not find evidence that the variational patterns in the Mexican towhees may readily be interpreted as due to the same causal factors. In the rock nuthatches selection against interspecific responses has resulted in the reinforcement of characters (facial mask) which apparently function in species recognition, and in changes of feeding structures (bill) which act to reduce competition for food. It seems quite appropriate to call this "character displacement" in the sense intended by Brown and Wilson. In the towhees the situation is more complex. In some areas such as at Teziutlán and Pátzcuaro, introgression is, apparently, resulting in swamping of the differences between *ocai* and *erythrophthalmus* while in Oaxaca there is no evidence of hybridization. To complicate the picture further there is the low incidence of hybridization on Mount Orizaba and at Puerto Morelos. As previously noted, it does not seem possible to decide definitely whether introgression in these areas has not yet become extensive or whether selection is against the hybrids and reinforcement of isolating mechanisms is in progress. If such reinforcement should be occurring, it would be appropriate to call it "character displacement" due to selection against hybrids. This, as noted by Brown and Wilson (*op. cit.*: 49), is not a new concept. Because one of us (Sibley, 1957) has recently reviewed the problem in some detail, we prefer to refer interested persons to that review rather than to repeat the discussion here. We may say that we find no serious disagreement with the idea of "character displacement" when equated with the concept of "reinforcement." This concept was first proposed by Fisher (1930), discussed by Sturtevant (1938), and it has been developed in detail by Dobzhansky (1940, 1951).

Brown and Wilson (*op. cit.*:62) call attention to the danger of using the greater variability of a population as an indication that it is of hybrid origin. We acknowledge this danger and agree further with the comments by Miller (1955:11) on the subject. To support their belief that high variability is not always a reliable criterion for the identification of a hybrid population, Brown and Wilson cite data on the size of the tail spot in the populations of *Pipilo erythrophthalmus* studied by Dickinson (1952). Brown and Wilson note that the coefficient of variation in this character is 12 in the northeastern United States and 22 in the Florida population. Since these are areas far removed from the influence of *ocai* these high coefficients of variation cannot, say these authors, be ascribed to hybridization. We agree that hybridization is not involved in this instance, but neither is the variability of the tail spot in the Florida race significantly greater than in the other populations of *erythrophthalmus*. Brown and Wilson have here fallen into a common error in the application of the coefficient of variation. It is simply this.

The coefficient of variation is a measure of variability relative to the mean. This statistic has several faults and limited usefulness. For example, if the standard deviation remains constant and the mean increases, then the coefficient of variation simply decreases as the mean increases. If the mean is a constant and the standard deviation

changes, then a comparison of the coefficients of variation is identical with a comparison of the standard deviations except for division by a constant. In some situations, there is a linear relationship between the mean and the standard deviation and, although both decrease, they may decrease at the same rate resulting in the same value for the coefficient of variation. In these instances the coefficient of variation is of some usefulness. However, if one wishes to consider the variability of a character in several subspecies the mean and standard deviation should be examined separately. The mean gives information on the mean value of the population while the standard deviation gives information on the variability in the population.

Using Dickinson's (1952) data on the size of the tail spot, Bartlett's chi-square test for the homogeneity of variances (Snedecor, 1946:251) was computed for the four variances obtained for males and for the four variances obtained for the females. In neither case was the chi-square value large enough to be declared significant at the 5 per cent level. In fact, the probability of obtaining chi-square values as large or larger than those obtained was between .15 and .20 for both sexes. These facts simply mean that the variability in the tail-spot size of Florida towhees is not greater than that in other populations of eastern North America. The example chosen by Brown and Wilson is thus without foundation as a basis for criticism.

The tail-spot size in the Mexican towhee hybrids has been used and measured in a somewhat different fashion from that employed by Dickinson. The latter actually measured the size of the spot in millimeters. In the Mexican hybrids, we have merely assigned specimens to one of five categories on the basis of the "clarity" or "clouding" of the spots. In pure *P. erythrophthalmus* the tail spots are clear white. The influence of *ocai* is indicated in hybrids by progressive clouding with dusky or greenish coloration. Pure *P. ocai* has an unspotted solid green tail. It may be noted that Davis (1957) has shown that the width of the white spot on the fourth rectrix of *P. erythrophthalmus* is smaller in first-year birds than in adults. This should be considered if actual measurements of tail-spot size are used. The method used in scoring *erythrophthalmus* x *ocai* hybrids seems not to be seriously affected by this discovery.

The comments of Brown and Wilson (*op. cit.*:62) concerning the occurrence of chestnut in the pileum of *P. erythrophthalmus* in areas far removed from the Mexican hybrid zones were apparently based upon Dickinson's (1952:332) data. On this point we have nothing to add beyond the discussion in a previous paper (Sibley, 1954:288).

SUMMARY

A collection of 338 specimens representing the Rufous-sided Towhee (*Pipilo erythrophthalmus*), the Collared Towhee (*P. ocai*), and hybrids between them was made in eastern México in 1954. Hybrid populations were analyzed using the "hybrid index" system and measurements of size and weight were made.

Reference to the map, figure 1, will provide a summary of the distribution of populations and their average hybrid indexes. Of particular interest is the situation on Mount Orizaba where the two species are sympatric with a low incidence of hybridization although the Orizaba *ocai* population is in genetic contact with the hybrid population at Teziutlán only 65 miles to the north. In Oaxaca, the two species occur in sympatry with no evidence of hybridization yet found in 96 specimens.

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Department of Conservation, Cornell University, Ithaca, New York, July 15, 1957.

MORNING AND EVENING SONG OF ROBINS IN DIFFERENT LATITUDES

By ROBERT C. MILLER

The singing of male robins (*Turdus migratorius*) in the breeding season occurs, in middle latitudes, intermittently throughout the day, but it is maximal in the early dawn, and it reaches a second though lesser peak in the evening shortly before the birds go to roost. These periods of concentrated singing are sufficiently well marked to be designated morning song and evening song, and they are regular enough to be predictable from day to day with an accuracy of from one to a very few minutes.

In the latter half of June, 1957, the writer made an automobile trip from Berkeley, California, to Fairbanks, Alaska. Since these localities represent a difference of about 27 degrees of latitude, it seemed worth while to make some observations en route of the times of morning and evening song of robins. The dates were propitious in that they represented a few days before and after the summer solstice, a period when the days are longest and when their length is changing very slowly. Between June 15 and 30, the time of sunrise at Berkeley changed only 3 minutes, and at Whitehorse, Yukon Territory, it changed only 5 minutes. Thus the differences observed in the times of morning and evening song are clearly due primarily to latitude.

For the observations recorded here, the end of evening song is the time at which the last robin song was heard. The beginning of morning song is the time at which the first robin song was heard. The end of morning song is not so easily determined, because it does not end abruptly but trails off into intermittent singing. Sometimes an individual robin will continue singing for some minutes after all others within hearing have ceased. Not infrequently birds which have become silent will resume singing for a short time. The end of morning song has been recorded as the time at which *all* or *most* of the robins in a given locality became silent for one or more minutes.

Since the time of the end of morning song is to some extent a matter of the observer's judgment, these data are regarded as the least reliable. However, both the magnitude and trend of the differences recorded suggest that in general they are outside the limits of error of observation. No attempt was made to record the beginning of evening song; this proved impracticable because of the logistic problem of finding food and lodging at the end of a day's travel.

Whitehorse, Yukon Territory, was the point farthest north at which data could be obtained on this trip. When I arrived at Fairbanks (65°N) on June 30, the season there was farther advanced, and robins had finished nesting and had ceased singing. On July 1, at 1:58 a.m., one robin sang for three or four seconds. This was the only robin heard in the course of two days spent in the vicinity of Fairbanks, although the birds were seen in abundance.

The question may arise as to whether robins were still nesting at Whitehorse on June 28–29. Evidence that they were is provided by their early morning singing, and by the fact that one robin was seen carrying something in its bill, presumably feeding young. There is some possibility that the lack of evening song may have been due to a tapering off of the nesting season, although that is not my present interpretation.

An inspection of the data in table 1 indicates certain overall trends, to which the observations at Hope and Williams Lake, British Columbia, pose certain anomalies. Although the difference in latitude between Bellingham, Washington, and Hope is minor (38′), evening song at Hope ended 11 minutes later than at Bellingham, while morning song was one minute shorter in duration. The latter difference is negligible; but both

Table 1

Morning and Evening Song of Robins at Different Latitudes
(All readings converted to mean local time)

Place	Date (1957)	Latitude	End of evening song	Beginning of morning song	End of morning song	Duration of morning song
Berkeley, Calif.	June 16	37°52′N	8:51 p.m.			
	June 18			3:40 a.m.	4:22 a.m.	42 min.
Bellingham, Wash.	June 21	48°45′N	8:36 p.m.			
	June 22			2:47 a.m.	3:44 a.m.	57 min.
Hope, B.C.	June 22	49°23′N	8:47 p.m.			
	June 23			2:43 a.m.	3:39 a.m.	56 min.
Williams Lake, B.C.	June 23	52°11′N	(None)			
	June 24			2:35 a.m.	3:30 a.m.	55 min.
Dawson Creek, B.C.	June 25	55°46′N	8:27 p.m.			
	June 26			(Before* 1:58 a.m.)	3:01 a.m.	(More than 63 min.)
Ft. Nelson, B.C.	June 26	58°49′N	7:51 p.m.			
	June 27			1:18 a.m.	2:38 a.m.	80 min.
Whitehorse, Yukon Ter.	June 28	60°43′N	(None)			
	June 29			0:58 a.m.	2:27 a.m.	89 min.

* Robins already singing when observations began.

differences are, when compared with the general trend of the data, in the wrong direction. This may be due to the location of Hope, which is surrounded on three sides by mountains but is wide open to the west, looking down the Fraser River valley. This situation would tend to shorten morning twilight and extend evening twilight.

Observations at Williams Lake were unsatisfactory because of a scarcity of robins in the vicinity. None was seen or heard in the evening. But at 2:35 a.m. two robins began singing and continued until 3:30 a.m., after which both were silent. At 3:31 a.m. a third robin, in a different place, began singing, continued for 14 minutes, and then ceased. On the basis of the criterion used at other localities (all or most robins silent for at least one minute), this last bird was excluded from the table, an admittedly arbitrary procedure. If there had been a dozen robins singing in the vicinity, it is highly likely that the one-minute silence would have been bridged and I would have recorded the duration of morning song as substantially longer. The behavior of this "lazy" robin raises an interesting point. Is morning song a continuous performance by individual birds, or do they, so to speak, sing in relays?

At Bellingham I was able to keep an individual robin under observation for 39 minutes, during which time it sang from three different perches, interrupting its song only briefly while flying from perch to perch. At Williams Lake two robins sang for 55 minutes, with only such pauses as are normal to the phrasing of the song. At Dawson Creek and farther north, however, I gained a definite impression that different birds were singing at different times, and that the lengthened time of morning song was due at least in part to the overlapping of the songs of different individuals. In latitudes where morning twilight is short, all robins become active at about the same time; but it seems likely that in northern latitudes, where the twilight is longer or the sky is light all night, the morning awakening and accompanying song is distributed over a longer period.

The singing behavior of robins in high latitudes that have perpetual daylight in June would be an interesting subject for investigation. The northerly distribution of robins extends well beyond the Arctic Circle. John E. Campbell (personal communication) noted robins singing at Bettles, Alaska, 25 miles north of the Arctic Circle, at midnight on June 8, 1957, and at Anaktuvuk Pass (lat. 68° 15′ N) at 1:00 a.m. on June 11. In

each instance several robins were heard and their singing was continuous over a period of time—typical morning song.

In middle latitudes the evening song of robins is not as striking and well developed a type of behavior as morning song. The observed relation between the end of evening song and latitude is erratic, but on the whole it appears that evening song terminates earlier as one goes north. If morning and evening song were exact reciprocals, they would merge at some high latitude. This apparently does not occur.

Too much weight should not be given to the single observation at Whitehorse. But there is at least a suggestion that, in latitudes where morning song begins soon after midnight, evening song as a recognizable entity disappears.

From the data reported here, it can be concluded definitely that, between the latitudes of approximately 38°N and 61°N, in the latter half of June, the morning song of robins begins progressively earlier and ends progressively earlier, with increase of latitude. The evidence is also strong, with the exceptions noted, that the duration of morning song increases with latitude. It is provisionally suggested, subject to further investigation, that evening song tends to terminate earlier at higher latitudes, and that at some latitude north of 58°N it may disappear altogether as a distinct entity.

California Academy of Sciences, San Francisco, California, October 21, 1957.

DISTRIBUTION AND MIGRATION OF RACES OF THE MOURNING DOVE

By JOHN W. ALDRICH and ALLEN J. DUVALL

The Mourning Dove (*Zenaidura macroura*) is a widespread species in North America except in the boreal region. It breeds regularly from the Atlantic to the Pacific and from the non-boreal sections of southern Canada south to central México and the Greater Antilles. It is reported to breed locally southward in Central America (Eisenmann, 1955:36) even as far as Panamá (Griscom, 1935:310; Wetmore, 1956:124). Its habitat ranges from the highly mixed and diversified assemblage of trees, shrubs, and openings of suburban and rural residential areas to the extensively open grasslands of the Great Plains. In fact, this species includes within its breeding habitat most ecological types except marshes and heavily wooded areas. The habitats which appear to support the denser breeding concentrations, however, are those associated with the more arid western portions of the continent, particularly the extensive grasslands of the Great Plains and the brush lands of the Great Basin and southwestern deserts. In the east, where deciduous forest is the natural vegetation, Mourning Doves are much less abundant and they occur in greatest numbers in the more open farming country.

THE PROBLEM

The Mourning Dove is a game bird in some sections, particularly in southern United States; in other parts of the country, it is valued more highly as a songbird. Because of its status as a game bird, the United States Fish and Wildlife Service is especially concerned with evaluating the increases and decreases in population which may occur in any part of the Mourning Dove's range. Various methods are being explored for obtaining indices of abundance and for determining how breeding populations of different abundance levels are related to the migrant populations which provide game birds in some parts of the country. One of the methods being explored for determining the relative contributions of Mourning Dove breeding areas to the localities where shooting must be controlled is to analyze the racial types represented among the birds which have been killed by hunters. The value of this approach is of course dependent upon how much geographic variation exists in the species and how consistent that variation is. In some respects it is less satisfactory than the banding method, but in the absence of adequate samples of breeding populations that have been banded and recovered, the analysis of racial components is the only source of information on migration. In 1950, the senior author attempted to make such a study in Florida by comparing, in the field, the doves in hunters' bags with Mourning Dove skins representative of the known races (Aldrich, 1952). This same technique was attempted in the fall migration seasons of 1951 and 1952 in Texas.

These attempts to determine the breeding areas represented by the doves in hunters' bags showed the lack of information on geographic distribution in the breeding season of the various color types observed among the hunted birds. This provided the main stimulus to find geographically variable characters which would enable us to pinpoint much more definitely the origin of these doves.

PROCEDURE

The first step was to sort out all of the breeding specimens of Mourning Doves in the United States National Museum, including those in the Fish and Wildlife Service collection. Only specimens taken in late May, June, and July were selected as representatives of breeding populations because of the known continuation of spring migration past the middle of May and the beginning of fall migration in early August (Austin,

1951:157). Although Dahlgren (MS) considered June to be within the spring migration season in Utah, we believe that June migration occurs so infrequently that the large majority of specimens taken in that month would be valid. With this exacting criterion of "breeding specimens," it was soon obvious that the number of specimens would be far too scanty, particularly from the eastern states.

The next step was to borrow as many specimens as we could to fill the gaps in our breeding series. For very helpful cooperation in the lending of specimens, we are indebted to the curators or owners of the following collections: Alabama Cooperative Wildlife Research Unit; American Museum of Natural History; California Academy of Sciences; Chicago Natural History Museum; Joseph Moore Museum, Earlham College; Louisiana State University Museum of Zoology; Minnesota Museum of Natural History; A. F. Ganier, Nashville, Tennessee; Museum of Comparative Zoology; Cleveland Museum of Natural History; Museum of Vertebrate Zoology; University of Kansas Museum of Natural History; University of Michigan Museum of Zoology; University of Wisconsin Zoological Department; and M. G. Vaiden, Rosedale, Mississippi. Even with all of the specimens we could assemble by borrowing we still lacked material from critical areas, particularly those in the midwest and south. Collection of specimens from these areas was done by the junior author, assisted by Gorman M. Bond, between May 25 and June 19, 1953. In this period, 7700 miles were traveled by auto, an average of almost 300 miles per day, and 129 specimens were collected in 12 states. These were shipped in dry ice to Washington where they were prepared for study. In addition, Thomas D. Burleigh, of the United States Fish and Wildlife Service, made special trips to collect breeding doves in the northwestern states and he proceeded east as far as Wisconsin. C. C. Anderson, of the Florida Game and Fresh Water Fish Commission, collected six breeding specimens, specifically for this study, at West Palm Beach, Florida.

Thus we were ready to attempt the analysis of geographic variation with 204 breeding specimens from continental United States, two from México, six from Panamá, and 21 from the Florida Keys and the West Indies. Because of the paucity of summer-taken birds from this last area, doves taken from April through July were used for comparison.

GEOGRAPHIC VARIATION

Conclusions from our analyses show that there are four main types of morphological variation in Mourning Doves; these types are geographic and they are distinguishable in all sex and age plumages. The most distinct and consistent trend, at least on the continent, is in tone of coloration, from dark in the east to pale in the west. There is a trend in length of wing from shorter in the tropical region to longer in the northern areas. In progressing westward on the continent there are trends toward increasing bill length and decreasing toe length. There is a slight trend within the United States from more brownish coloration in the south to more grayish in the north. This last is probably better defined as a condition of "color phase" which tends to occur in slightly different frequencies geographically. Thus there are more gray birds in the north and more brown birds in the south. In addition to the main continental variations of size and intensity of color we find deep buff-bellied underparts associated with small size in the birds of the West Indies and the Florida Keys, and relatively large bills and feet associated with very deep brownish coloration in the birds of Clarión Island off the west coast of México. There are other less well defined differences in linear proportions which show up in the statistical analyses of measurements (table 1, and figs. 1 and 2). In all measurements it was noted that males have significantly larger wing, middle toe, and tarsus measurements than females when large samples are compared. Taking all of the noted variations into consideration, there seem to be only five combinations which are distinct enough

to permit the reasonably sure identification of a large majority of any population and which warrant their being called separate races. These races are:

1. The long winged, dark population of eastern United States and southern Ontario —*Z. m. carolinensis.*

2. The long winged, pale population of western United States, southwestern Canada, and temperate México—*Z. m. marginella.*

3. The short winged, short legged, long billed, pale population of Panamá and possibly other parts of Central America—*Z. m. turturilla.*

4. The short winged, dark to medium toned, deep buff-bellied population in the West Indies and Florida Keys—*Z. m. macroura.*

5. The relatively large footed, large billed, very dark brownish population on Clarión Island of the Revilla Gigedo group, off the Pacific coast of México—*Z. m. clarionensis.*

Table 1

Measurements of Races of *Zenaidura macroura* Based on Breeding Specimens Only

		Wing				Culmen			
Subspecies	Sex	Sample size	Range	Mean	Standard error	Sample size	Range	Mean	Standard error
marginella	♂	118	137.0–156.5	144.3	.34	107	12.0–16.5	13.5	.08
	♀	36	131.5–154.0	141.7	.79	34	12.0–15.0	13.5	.01
carolinensis	♂	34	136.5–154.0	144.8	.73	32	12.0–14.5	13.3	.13
	♀	17	130.5–143.0	137.9	.97	17	12.0–15.0	12.9	.23
macroura	♂	11	135.5–140.0	137.8	.52	11	12.0–13.5	12.8	.14
	♀	10	125.5–136.0	132.4	1.04	10	11.0–14.5	12.8	.32
*turturilla**	♂	4	135.0–142.0	138.9	1.48	4	13.5–14.0	13.9	.13
clarionensis	♂	4	136.0–146.0	139.9	2.12	4	15.0–15.5	15.1	.13
	♀	3	134.0–138.0	136.7	2.70	4	13.5–16.5	14.9	.69
			Tarsus				Middletoe		
marginella	♂	114	19.5–23.5	21.3	.07	117	18.0–22.0	19.9	.08
	♀	35	19.5–21.5	20.5	.01	36	17.5–21.0	19.2	.01
carolinensis	♂	34	19.5–23.0	21.5	.39	34	19.0–23.0	20.5	.19
	♀	17	19.5–21.5	20.7	.19	17	18.0–21.5	19.4	.21
macroura	♂	11	20.0–23.0	20.9	.31	11	19.0–21.5	20.2	.22
	♀	10	18.0–21.5	20.0	.34	10	16.0–20.5	19.1	.44
*turturilla**	♂	4	19.0–20.0	19.8	.02	4	20.0–21.0	20.4	.02
clarionensis	♂	4	22.5–24.5	23.5	.46	4	22.5–24.0	23.1	.31
	♀	4	21.5–23.5	22.3	.43	4	22.5–23.5	23.0	.20

* Only one female specimen of *turturilla* was available for measurement. This had: wing, 127.0; culmen, 14.0; tarsus, 19.5; middle toe, 19.0.

The various measurements for each race differ disproportionately. One race may have a larger wing but a shorter bill than another whereas a third race may have a larger middle toe but a shorter tarsus. Significant differences in these proportions are brought out by a statistical analysis and graphing of the measurements by Aelred D. Geis of the Waterfowl Biometry Office of the United States Fish and Wildlife Service. To indicate the variability in measurements the standard error was calculated for each mean. Confidence limits were then calculated at the .05 probability level as the mean ± "t" times the standard error. These confidence limits, the means, and the ranges are indicated in figures 1 and 2. Where the confidence limits do not overlap, statistically significant dif-

ferences are indicated. When this procedure indicated nearly significant differences, analysis of variance was used to test the significance of the differences.

Z. m. marginella.—Statistically, wing measurements were significantly longer than in all races except *clarionensis* and male *carolinensis*. Culmen length was significantly longer than in *carolinensis*

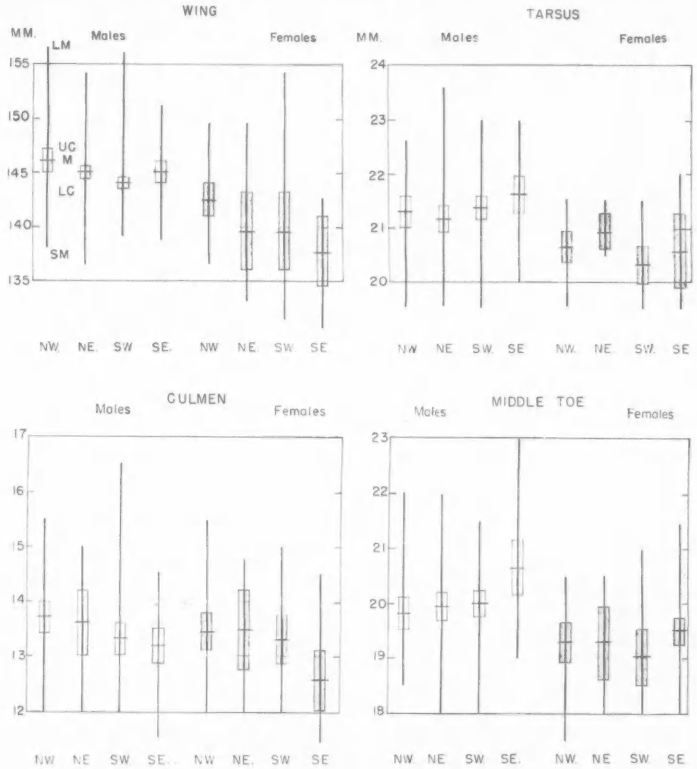

Fig. 1. Comparison of measurements of breeding specimens of *Zenaidura macroura*. NW= Washington, Oregon, Idaho, Montana, Wyoming, North Dakota, South Dakota, and Nebraska; NE = Minnesota, Iowa, Illinois, Indiana, Ohio, Pennsylvania, New Jersey, and to the north and east; SW = California, Nevada, Utah, Colorado, Kansas, Oklahoma, Texas, New Mexico, and Arizona; SE = south of NE area and east of SW area.

and *macroura*, and it was significantly shorter than in *turturilla* and *clarionensis*. The length of the tarsus was significantly longer than in *turturilla* and shorter than in *clarionensis*. The tarsal length was not significantly different from the other races. The middle toe was significantly shorter than in *carolinensis, turturilla,* and *clarionensis* but it was not different from that of *macroura*.

Z. m. carolinensis.—Females had significantly shorter wings than in *marginella*. The wings were significantly longer than in *macroura* and *turturilla* but they were not significantly different from those of *clarionensis*. Culmen length was significantly shorter than in *marginella, turturilla,* and *clarionensis* but it was not significantly different from that of *macroura*. In tarsal length this race differed significantly only from *turturilla,* which was smaller. The average middle toe length of this race was significantly longer than in *marginella* and very significantly shorter than in *clarionensis*.

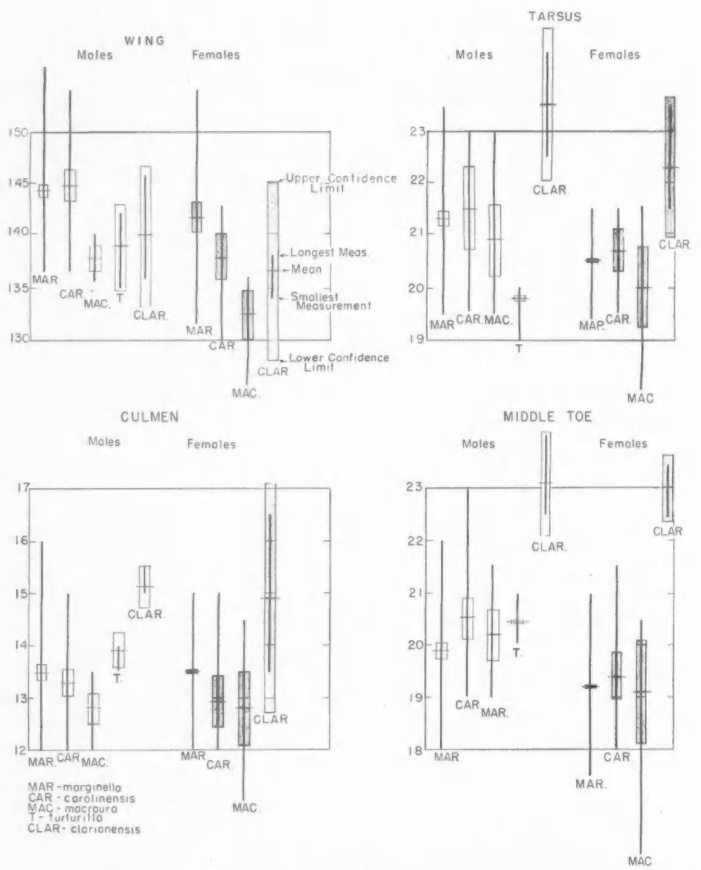

Fig. 2. Measurements of races of *Zenaidura macroura* based on breeding specimens.

Z. m. macroura.—The wing measurements of this race were significantly shorter than in *marginella* and *carolinensis*. Culmen length was shorter than in all races except *carolinensis*. The tarsus was significantly longer than in *turturilla* and shorter than in *clarionensis*. The middle toe measurements were significantly different only from those of *clarionensis*, which were much longer.

Z. m. turturilla.—A sample of only four males was available. The wings of this race were significantly shorter than those of *marginella* and *carolinensis*. Culmen length was significantly shorter than in *clarionensis* and longer than in *macroura*. It is possible that a larger sample would have indicated a significantly longer culmen than that of *marginella* and *carolinensis*. The tarsus of *turturilla* was significantly shorter than in all other races. The middle toe differed significantly only from that of *marginella*, which had smaller toes, and *clarionensis*, which had much longer toes.

Z. m. clarionensis.—The wing measurements did not differ significantly from any other race based on the small sample of four birds of each sex. Lengths of culmen and middle toe averaged significantly longer than in all other races. The tarsus was significantly longer than in all races except *carolinensis*.

The identifications of specimens examined in accordance with the foregoing criteria

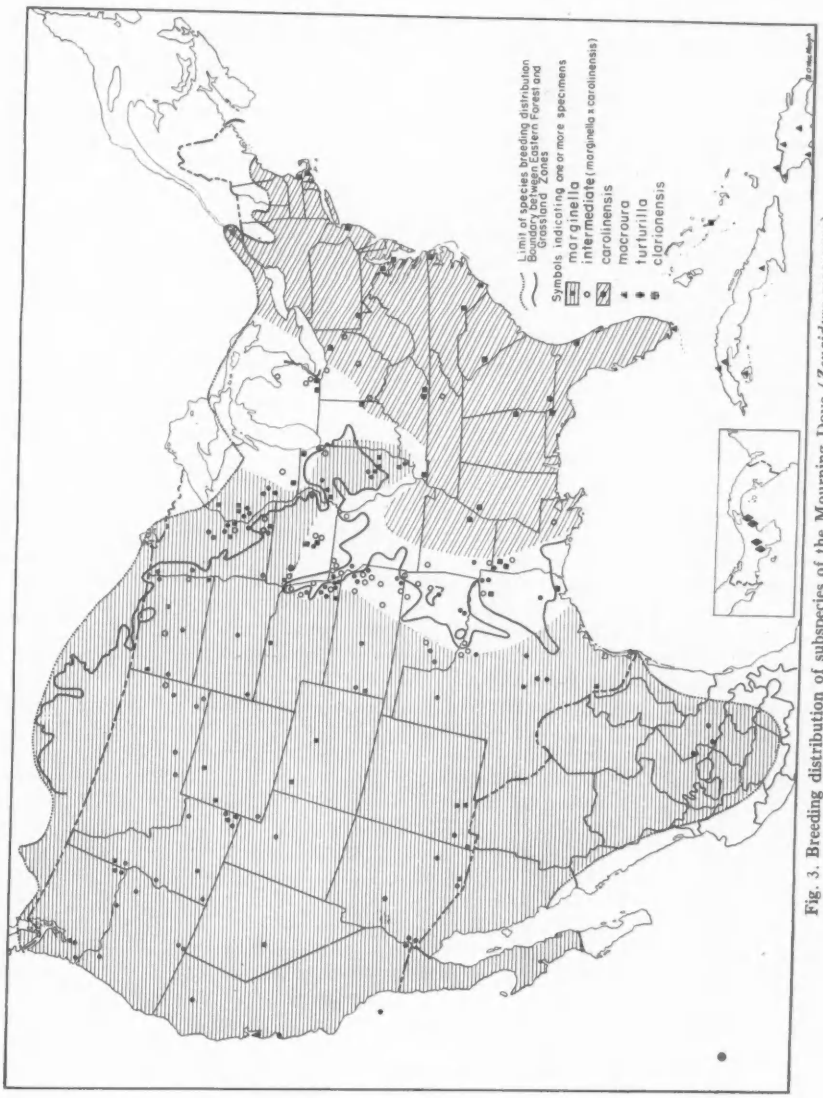

Fig. 3. Breeding distribution of subspecies of the Mourning Dove (*Zenaidura macroura*).

are shown in the list on pp. 122–126, and the localities of breeding specimens are shown on the map (fig. 3).

With the exception of a Central American race, the general and specific characters of all of the races recognized in this study have been described in detail by Ridgway (1916*a*:339–353). For this reason it would be repetitious to give detailed descriptions of each race here. It will suffice merely to point out how our findings differ from those contained in that important reference. We did not find a satisfactory difference in the size of the black spots and the extent of the metallic glossed areas listed as sex characters by Ridgway (*op. cit.*:343) although it is probable that average differences in these characters do exist. The smaller size and duller coloration, especially the duller, more brownish or drab and less vinaceous underparts of the females, as reported by Ridgway, are quite reliable. In addition, a rather reliable sex character is the relatively bright bluish-gray coloration of the dark areas on the occiput and hindneck of the males.

A difference between *Z. m. carolinensis* of the eastern United States and *Z. m. macroura* of the West Indies is the larger size of the former (*op. cit.*:345), but Ridgway's other characters of the upper parts averaging less brownish and the underparts paler (less darkly vinaceous) in *carolinensis* are not corroborated by the present study. The main color difference between these races, when compared phase for phase, is the less deeply buffy or rufescent coloration below in *carolinensis*, particularly on the belly. No reliable difference in the color of the upper parts of these races is evident, although the majority of the West Indian birds appear somewhat paler than typical *carolinensis* from the Atlantic seaboard of the United States.

Typical *Z. m. marginella* of western United States differs from typical *Z. m. carolinensis* from the east in the much paler coloration of the former throughout; it is not merely "slightly paler" as expressed by Ridgway (*op. cit.*:347). The slightly larger size of *marginella* has generally been considered a character distinguishing it from *carolinensis* (*op. cit.*:347; Rand and Traylor, 1950:179). This is only partly borne out by our measurements. Males show no difference in wing length, although there is an indication of a smaller wing in the small sample of female *carolinensis* and a shorter bill in both sexes (table 1, and fig. 2). On the other hand, there is an indication that *carolinensis* has a larger foot (see toe measurements, table 1, and fig. 2).

The coloration of the back and lesser wing coverts of typical examples of *carolinensis* ranges from a cinnamon brown to a dark Saccardo's umber as in Ridgway (1912:pl. XV) or yellowish, yellow-red 7.5YR–5/4 according to Munsell Color Company (1942). The range in color of typical *marginella* is light Saccardo's umber to buffy brown or yellow-red 10.0YR–6/4 of these same authorities.

When samples of *carolinensis* and *marginella* are selected from well within their breeding ranges, little or no overlap in color characters occurs. Examples from the area of intergradation, of course, show all degrees of overlap. Study of the list of specimens examined (p. 122) discloses what appears to be a complete breakdown of racial segregation within the states located in the zone of intergradation. For example, among the breeding specimens taken in Missouri, one was identified as *carolinensis*, five as intermediate, and five as *marginella*. This type of mixture is found all along the highly interdigitated ecological boundary between natural prairie and woodland from Texas to Michigan (see discussion under Ecological Distribution). This complicates the identification of migrants and it makes completely impossible the identification of many specimens as being definitely from a geographically intermediate zone. Thus, it would seem imperative that separation of geographical intermediates, as well as non-breeders, be made from samples before applying any percentage of separability rule for subspecific validity as was attempted for these subspecies by Rand and Traylor (1950:179–181).

Where only breeding specimens are used, based on the June and July criterion and taken from areas beyond the intermediate zone (fig. 3), a very high percentage of specimens of *carolinensis* can be distinguished from an equally high percentage of *marginella*. In fact, in our samples, only one specimen from the range of *carolinensis* and one from the range of *marginella* appeared to have the characters of the opposite race. The character separating *marginella* from *carolinensis*, and the truly intermediate specimens from typical examples of either race, is as easily detectable in a separate wing as it is in complete skins. Thus, it is practical to separate these components of hunters' bags on the basis of wing samples.

We were unable to verify Ridgway's (1916*a*:348, footnote) characterization of a distinct subspecies in the Cape San Lucas district of Baja California. No breeding specimens from there have been seen by us, nor did Ridgway examine any. In fact, the species is not now considered to breed that far south in Baja California (Friedmann, Griscom, and Moore, 1950:116). The brown coloration noted by Ridgway as the distinguishing character seems to be somewhat more prevalent among specimens from the arid southwest. However, as pointed out previously in the present paper, this condition is interpreted as that of a color phase which may appear anywhere but which tends to be more prevalent in the southwest than elsewhere.

The existence of a "very distinct form peculiar to the humid coast district of Oregon and Washington" and named *caurina* by Ridgway (1916*a*:348, footnote) likewise could not be substantiated. The type specimen, United States National Museum 12540 (not "No. 22540") is certainly a very deeply colored specimen when compared with typical examples of *marginella*; in fact, it approaches the richly colored race *clarionensis* in this respect. There is no approach to this race in large size of bill and feet, however, and the over-all resemblance is greatest to *carolinensis*. Cassin (1858:278), in his report on the Wilkes collection, whence this specimen came, reported that specimens of Mourning Doves from Oregon present no characters different from those of the common bird of the states on the Atlantic coast and he noted that they differed from the "smaller species" (*Ectopistes* [= *Zenaidura*] *marginella*) discovered by Woodhouse (1852). This would imply that Cassin saw more than one specimen from the Wilkes collection although there is no evidence of this in his catalogue, which lists only the specimen to which he applies the number 561.

Whether or not the type of *caurina* (a dismounted specimen without an original field label) came from the breeding population of the "humid coast district of Oregon and Washington" cannot be determined from the incomplete information available to us. We lack information on both the date and the exact locality where it was collected. In addition to the red type label of the National Museum, it bears a large card label obviously removed from the base on which the specimen had been mounted. On this label is printed: "U. S. Explor. Exped. Capt. C. Wilkes, U.S.N.—Oregon—T. R. Peale." In handwriting on this label is the number 451 which refers to a species number used in a list of North American birds (Baird, 1858:xliv). In his report on the expedition on which this specimen was collected, Peale (1848:189) commented that the species was observed in Oregon on the Columbia River and listed the specimen in his catalogue under the number 571. The entry in the National Museum catalogue for this specimen, no. 12540, originally made on July 15, 1859, gives the additional following information: "Presented to Chicago Acad. Sci. Jan. 28, 1881." It evidently was returned subsequently to the National Museum. It therefore appears that the type of *caurina* was collected on the Columbia River, probably not far upstream from the Pacific coast, and that there may have been one or two other specimens from that locality in the collection although they are not now extant in either the United States National Museum or in the Philadelphia

Academy of Sciences (de Schauensee, personal communication). There seems no way now of more definitely establishing the locality and time of year of collection. If this specimen was representative of the breeding Mourning Doves of the coastal strip of Washington and Oregon in the early 1840's, that population has certainly become extirpated and replaced by a very much paler race as suggested by Jewett, Taylor, Shaw, and Aldrich (1953:340). Breeding specimens collected west of the Cascades in Washington by Thomas D. Burleigh in late May, 1954, specifically to determine this point, and a specimen in the University of Washington collection taken at Tacoma, June 14, 1913, are typical *marginella*. Burleigh (personal communication) remarked that doves breed rarely in that area today. Slipp (1941:59) summarizes the occurrence of Mourning Doves in the Pacific Northwest and indicates that they have been rare in western Washington since Cooper (1860:219) reported taking many specimens at Fort Steilacoom in the 1850's.

The race *tresmariae*, described by Ridgway (1916*b*:107) from María Madre Island, Tres Marías group, Nayarit, off the Pacific coast of México, is of doubtful validity. First, the type collected by Nelson and Goldman on May 5, 1897, is the only known specimen from the Tres Marías Islands. Further, Nelson (1899:36) said that only a few other Mourning Doves, in addition to the one collected, were seen on the island in the first part of May, and he concluded from their behavior that they were "probably stray migrants." Subsequent visitors to those islands have not recorded the Mourning Dove there (McLellan, 1926:294–295; Kenneth E. Stager, personal communication). In appearance, the type of *tresmariae* is quite typical of *Z. m. carolinensis* except in the intensity of the cinnamon rufous on the forehead and sides of the head. In these respects, it is not quite matched by any specimen from the east. It might be considered as exhibiting intermediacy between *marginella* and the deeply colored *clarionensis* (Townsend, 1890:133) of Clarión Island, which is in line with but farther offshore than the Tres Marías. However, there is no approach to the large heavy bill and feet of that race. In view of the lack of evidence of a breeding Mourning Dove population either past or present on the Tres Marías Islands, it is more likely that the type was a stray individual from some breeding population of dark brownish birds, and probably it came from within the range of *carolinensis*. Other dark specimens which have been noted in the present study from areas where one would expect to find *marginella* are: one taken at Laguna, San Diego County, California, June 15, 1894 (another from the same locality and taken on the same date is typical *marginella*); one at Mountain Spring, San Diego County, California, May 15, 1894; one at Baird, California, May 29, 1883; one at New Meadows, Adams County, Idaho, July 22, 1929; one at Hilger, Montana, August 4, 1919; one at Glendive, Montana, May 5, 1916; one at Jarilla Mountains, New Mexico, September 13, 1903; and one at Big Hatchet Mountains, New Mexico, July 19, 1908. However, among these, only the bird from Big Hatchet Mountains is considered as too dark to be within the range of variation of *marginella*.

Swarth (1922:209) reported a specimen taken at the mouth of the Stikine River, southeastern Alaska, which was so dark that he referred it to *carolinensis*, although he suggested that it might be referable to "the coastal subspecies *Z. m. caurina*" discussed previously.

The single specimen seen from the Bahama Islands, taken July 16, 1903, on Long Island, appears to be typical *carolinensis* without any indication of intergradation toward *macroura*. This specimen, taken well within the breeding season, is the only specimen seen from those islands in this study and therefore it constitutes the only first hand information we have for considering the Bahama Islands within the breeding range of *carolinensis*. It has been so considered previously by Peters (1937:84) and by Hellmayr

and Conover (1942:478). Although Bond (1956:65) lists 11 islands in the Bahamas on which *carolinensis* has been recorded, he does not say whether or not it breeds on any of them.

A single specimen collected at Sherwood Plantation, Brady County, Georgia, July 21, 1953, by Herbert Stoddard, is typical *marginella* in every respect. It was indicated on the label as "breeding" and the outline of the testes drawn on the label indicated well developed gonads. However, another specimen from the same locality taken on July 22, and other breeding specimens taken in the general area, are all typical *carolinensis*. The specimen taken on July 21 exhibits one character which indicates that it was not a breeding adult; this is the fresh, unworn condition of the tips of the primaries. In view of this fact, it would seem probable that this bird was a Mourning Dove which was out of its normal breeding area.

The specimen identified as adult *carolinensis*, taken on July 19 at Big Hatchet Mountains, New Mexico, may have been a similar instance of a non-breeding wanderer, either from the east or from an unknown, dark population in the west. It may be seen from the map (fig. 3) that other specimens from that general area are typical *marginella*.

Bond (1956:65) gives the range of *Z. m. macroura* as Cuba, Isle of Pines, Hispaniola, Gonave Island, Tortuga Island, Jamaica, Puerto Rico, and Mona Island. From specimens examined in the present study, this distribution can now be extended to the Florida Keys.

Wetmore and Swales (1931:195) noted that birds from Tortuga Island, Haiti, were darker than those from other parts of that country. They also noted that two birds from eastern Cuba were darker than all other Cuban specimens. These differences in dark and light specimens in both Cuba and Haiti were noted in our study, but because of insufficient breeding material of the dark type we could not reach any conclusions. We segregated all specimens from the Dominican Republic, Haiti, Cuba, and the Florida Keys taken in April, May, June, and July, as probably largely representative of the breeding populations in those areas. With this restriction of material, only the three birds from the Florida Keys and one from Mariel, Cuba, the type specimen of *Z. m. bella* (Palmer and Riley, 1902:33), were of the dark type. It is possible that these birds may represent a race of the humid coastal areas which is distinct from the population of the drier interior. This problem should be studied further after collection of breeding birds from such areas. Until this is done, we have no alternative but to follow the example of Wetmore and Swales (1931:195) and consider the color difference in the West Indian birds as individual variations. Thus we must continue to consider *Z. m. bella* as a synonym of *Z. m. macroura*. Wetmore and Swales (1931:195–197) seem to have resolved the confusion concerning the application of the names *macroura* and *carolinensis* satisfactorily by their restriction of the type locality of *macroura* to Cuba. If further subdivision of Cuban populations into races is subsequently found necessary, it will, of course, require further restriction of the type locality of *macroura*.

There seems to be no question concerning the correct application of the name *carolinensis* (Linnaeus, 1766:286) based on Catesby (1731:24). Catesby says of "The Turtle of Carolina" (Mourning Dove) that "they breed in *Carolina* and abide there always." Thus, the type locality of *carolinensis* has been designated as South Carolina by the American Ornithologists' Union (1931:153). Catesby's plate depicts a dull grayish colored dove which would be unidentifiable as to race.

The type specimen on which the original description of *Z. m. marginella* (Woodhouse, 1852:104) was based is a most disreputable looking object. It was a rather young bird in juvenal plumage. It is now without head or tail and has only one wing. The plumage is so extremely soiled that there is no chance whatsoever of identifying it with

any of the known racial types exhibited by birds in juvenal plumage. The specimen was collected September 6, 1850, by S. W. Woodhouse "in the cross timbers on the north fork of the Canadian [River, Oklahoma]." Specimens from that area collected subsequently have been mostly of the pale western type, although the breeding birds of the area tend to be intermediate. There is no way of knowing where this particular specimen was hatched since juvenal Mourning Doves wander far from their birthplace. However, the name *marginella* has long been associated with the western race of the Mourning Dove and, since this has good basis in precedent, the designation should be maintained despite the inadequacy of the type for establishing this point.

Neither the type specimen nor any of the type series of *Z. m. peninsulari* (Bailey, 1923) from Miami Beach, Florida, have been available for this study, but from the small wing measurements given by Bailey, particularly of the two males, it is believed that they may represent *Z. m. macroura*. That race is known to breed not far distant on the Florida Keys and it has previously been reported in the fall hunting season from the Miami area (Aldrich, 1952:450). Whether or not the type series of *peninsulari* represents the breeding population of the Miami Beach area cannot be determined because the dates of collection (all in February) were well within the migration period.

The southern limits of the breeding distribution of *Z. m. marginella* in México are given by Friedmann, Griscom, and Moore (1950:116–117) as latitude 26°N in Baja California, probably not farther south on the Pacific coastal plain than southern Sonora and the islands offshore, southward on the Central Plateau to Puebla (El Venerable) and Oaxaca (Tamazulapan), and probably nowhere on the Atlantic coastal plain in México. No substantiation could be found for the suggestion by Pitelka (1948:120) that the breeding doves of Oaxaca and Guerrero represent a dark race similar to *carolinensis*. It is believed that most, if not all, of the "dark" specimens examined by Pitelka were migrants from the north and did, in fact, represent the race *carolinensis*. Some of these same specimens were examined in connection with the present study and our determinations were divided between *carolinensis* and *marginella*. None of them, however, was considered to be breeding. The measurements of these specimens, which Pitelka (1948:121) thought were so small as to exclude *marginella,* are actually only slightly smaller than the average for that race according to our measurements.

South of the Central Plateau of México references to the breeding of Mourning Doves are very few and there is little information on their geographic variation. Eisenmann (1955:36) lists the Mourning Dove (without subspecific designation) as "breeding locally Mexico, Brit. Honduras, Honduras, W. Panama." It has been recorded as breeding near Dueñas, Guatemala, by Salvin and Godman (1902:243) and it has been found throughout the year in Costa Rica by Carriker, who considered the individuals that he saw retarded migrants from the north (Wetmore, 1956:125). Hellmayr and Conover (1942:477) mention specimens which they refer to *macroura* from Toledo District, British Honduras, October 17, and Divalá, Chiriqui, Republic of Panamá, November 11, 1900, as well as the record of breeding in Veraguas, Panamá, in 1925, also mentioned by Griscom (1935:310). Wetmore (1956) has made a special effort to collect this species in Panamá and to study its distribution in the field. He has added considerably to our knowledge of its range, which is now known to extend almost throughout the arid tropical savannas of the Pacific slope of Panamá from near the Costa Rican border almost to the Canal Zone. He named this population *Zenaidura macroura turturilla*.

The six Panamanian specimens examined in the present study are pale and they most closely approach *marginella* in this respect. They are small winged like the West Indian birds but they are paler than the average of *macroura*; they are somewhat grayer

and less intensely buffy on the underparts and they have a shorter tarsus and longer bill. They suggest a small variant of *marginella* in color but they are relatively long-toed. Since this extreme southern population differs from *marginella* merely in measurements, it may be assumed that other Central American breeding populations, which may occur between Panamá and the central Mexican tableland, are either referable to the same race as the population of Panamá or they are intermediate between it and typical *marginella*. We have no definitely breeding specimens from this area although we do have two specimens referable to *turturilla*, one from the Department of Santa Rosa, Guatemala, March 27, and one, date unknown, from Chinandega, Nicaragua.

ECOLOGICAL DISTRIBUTION

The ecological distribution of *Z. m. marginella* is given by Grinnell and Miller (1944:184) for California as mainly in the Lower and Upper Sonoran life zones, and sparingly in the Transition. Friedmann, Griscom, and Moore (1950:116–117) indicate a similar distribution in México by their designation of range as non-tropical areas up to 9000 feet in the mountains. This seems to be characteristic of the distribution of this race throughout its range. The ecological distribution of *Z. m. carolinensis* is similar to that of the western race in the equivalent eastern life zones—Austroriparian, Carolinean, and Eastern Transition.

From the standpoint of the correlation of racial differences with major ecological differences, it may be noted on the map (fig. 3) that the distinction between *carolinensis* and *marginella* follows roughly the distribution of the natural or climax vegetation areas of forest and grassland. In the ecotone area between grassland and forest, that is in the prairie woodlands and savannas, the breeding doves show a mixture of racial types or they are intermediate. This correlation is most noticeable in the southern and middle sections of the forest—prairie transition. Typical *marginella* extends eastward in the tongue of natural grassland known as the "Prairie Peninsula" as far as Illinois. It seems to break away from the normal ecological correlation in the extreme northern part of its range where it extends into the area of climax northern hardwood forest as far as central Wisconsin. One is led to speculate whether this latter situation was brought about by relatively recent occupation of the formerly heavily forested northern lands after these were opened up by lumbering, fires, and cultivation, thus making them suitable for invasion by breeding Mourning Doves. The most available source of an abundant breeding stock would have been the grasslands to the west and south occupied by *marginella*.

A further indication of the correlation of racial types with major ecological differences is that the southern limit of the breeding range of *marginella* is not known to descend into the Lower Tropical Zone either in the mountains of southern México or in the lowlands of either coast. Likewise, with the possible exception of a Bahama Island population, *carolinensis* is not known to breed in the tropical region. In fact, in the tropical region, represented by the Florida Keys and the Greater Antilles, *carolinensis* is replaced by *macroura*. Intergradation between *macroura* and *carolinensis* might be expected in southern Florida but no specimens are at hand to demonstrate this. The six specimens collected at West Palm Beach, Florida, August 8, 1956, are definitely *carolinensis* in color with only the small size of one of the two males to indicate possible intergradation toward *macroura*. Although the date of collection is outside our assigned limits for breeding specimens, the larger of the two males and one of the females had gonads in active breeding condition, and it is believed that all six birds represented the breeding population of that area. Thus, there is no definite sign of intergradation between *carolinensis* and *macroura* as far south as West Palm Beach, only 130 miles north of Plantation Key, where typical *macroura* breeds. This situation may result from a

possible invasion of the relatively recently exposed land of the Florida peninsula from the continent to the north by *carolinensis* and from the West Indies to the south by *macroura*.

The increase in wing length in proceeding northward from tropical to temperate regions is a good example of the ecogeographical principle known as "Bergmann's Rule" recently elucidated by Mayr (1956:105). In the United States this trend is continued within the race *marginella* as shown in figure 1 when northern and southern samples are compared.

In comparing tarsal and middle toe measurements of doves from the four quarters of the United States (fig. 1), there were no significant differences among the samples. However, the average wing length of doves collected in the northwest was significantly longer than that of birds collected in the southwest and the southeast. Also, the culmen length of birds collected in the northwest was greater than that of doves taken in the southeast.

MIGRATION

In the list of specimens examined (p. 122), it will be noted that there is a very extensive mingling of racial types in the course of migration and postbreeding wandering. Pale birds of the *marginella* type reach the Atlantic seaboard from New England to Florida and the West Indies while dark birds referable to *carolinensis* are noted far to the west. Probably these latter are responsible for the occurrence of dark specimens on the Pacific coast in Alaska and Oregon (type of *caurina*) and on the offshore islands of western México (type of *tresmariae*). Both races are reported in migration as far south as Panamá; *marginella* has been reported regularly and *carolinensis* once (Griscom, 1935:310).

An indication of the rather extensive postbreeding wandering of Mourning Doves away from their normal breeding range is the occurrence of these birds in Newfoundland, Labrador, Mackenzie, and Alaska. The records from Newfoundland are mostly for the fall although there is one as early as July (Peters and Burleigh, 1951:264), and there is one specimen in the United States National Museum taken in January. These specimens indicate that the birds which reach Newfoundland are mostly *carolinensis*, but one specimen, taken "Jan. — 1947," is intermediate between *carolinensis* and *marginella*. The nearest known breeding grounds of the former would be in northern New England and, of the latter, the eastern Great Lakes region. Six records for Labrador were reported by Austin (1932:144) for the months of June, August, September (2), and October (2). The record on June 5, reported by Austin, and the adult male specimen collected at Hay River, Great Slave Lake, Mackenzie, June 16, and examined in in the present study, although well within the breeding (or "non-migration") season, are assumed to be wandering, non-breeding individuals because of their great removal, both geographically and ecologically, from the normal breeding range of the species. Slipp (1941:60) and others mention a number of records from Alaska, ranging from July to November, but occurring mostly in September and October. The nearest known breeding area whence these birds might have wandered is in southwestern British Columbia.

The evidence, therefore, seems to indicate that the Mourning Dove is a highly mobile species that may move in any direction from its normal breeding area, when it is not actually engaged in nesting activities. Despite this fact, banding data indicate a high degree of fidelity of adults to the home area during the breeding season (Austin, 1951: 160; Quay, 1954:18). Further, the evidence from specimens seems to indicate that the bulk of the birds probably migrate in a generally north to south direction from the breeding areas to the wintering grounds; some individuals of northern origin migrate

as far south as Central America and the Greater Antilles. In reaching these far southern points there is an indication, from the concentrations of migrants in the southern tip of Texas (Texas Game, Fish and Oyster Commission, 1945:80) and on the Gulf coast of western Florida (Winston, 1954:35), that many of these doves are deflected by the Gulf of México and move around it in one direction or another, although there is some evidence that some birds fly directly across the Gulf (Bullis and Lincoln, 1952:36). In the more southern portions of the breeding grounds, including southern United States, a large part of the breeding population appears to be sedentary, individual doves moving very little from the place where they were hatched. The high percentage (75 per cent) of recoveries of banded doves within the same state in which they were banded, particularly in the south (Peters, 1956), is suggestive of this.

It can be readily understood from the above that the Mourning Dove, with its great differences in migratory habits in the various parts of its range, offers a particularly difficult subject for game management. To adequately protect all segments of the breeding population, it is essential to know where these segments are in the various seasons when hunting takes place. There is abundant evidence from game management reports that large concentrations occur during the fall migration in southeastern California and southern Arizona. Field work in connection with the present study has disclosed large migrant concentrations also in southern Texas and southern Georgia.

SUMMARY

The Mourning Dove is a widespread species breeding in the non-boreal regions of North and Middle America and from the West Indies south to Panamá. It is hunted extensively in many sections of the United States and in some sections of Canada, the West Indies, and México.

The trends in geographic variation of Mourning Doves are from dark coloration in the east to pale coloration in the west and from shorter wing length in tropical areas to longer in the temperate region. More rusty underparts are associated with birds of the West Indies, and extremely saturated coloration and relatively large bills and feet have been developed by the population on Clarión Island off the western coast of México. The combinations of geographic variation result in the recognition of five geographic races, two of which breed on the mainland of North America. The race *carolinensis* of eastern United States can be distinguished from the western race, *marginella*, by the color of the wings alone, which makes possible the recognition of these racial components from the wings of doves taken from hunters' bags.

Taking Ridgway's account in "Birds of North and Middle America" as a basis, discrepancies in the descriptions of sex and racial characters are pointed out. Two races recognized by Ridgway and one suggested as possibly distinct were not substantiated. The occurrence of dark and pale types among the West Indian populations are considered of possible racial significance, but sufficient breeding material is lacking to study the problem satisfactorily.

The allocation of type specimens and names to the various recognizable races which appears in the most recent literature is considered satisfactory.

The ecological boundaries between tropical and temperate life zones and between the western grasslands and eastern deciduous forest zones, generally speaking, separate distinct races from each other.

There is an extensive postbreeding wandering of birds in all directions, particularly northward, and there is an extensive mingling of racial types during migration.

Concentrations of fall migrants occur in certain areas in the southwestern states and both east and west of the Gulf of México.

LIST OF MOURNING DOVE SPECIMENS EXAMINED

In the following list, a. refers to adult, no juvenal plumage remaining; im. refers to immature, only a few juvenal primaries remaining, body plumage molt complete; jv. refers to juvenile, some juvenal body plumage remaining; brackets indicate that sex was determined by plumage coloration.

Zenaidura macroura marginella

MACKENZIE: Hay River, Great Slave Lake, June 16, 1908, ♂ a. ALASKA: Fort Yukon, Oct. 9, 1916, ♂ im. ARIZONA: Bisbee (7 mi. S), Sept. 14, 1892, ♀ jv.; Fort Huachuca (7 mi. SE), May 15, 1932, ♀ a.; Fort Lowell, Nov. 7, 1893 [♂] im.; Fort Whipple, July 2, 1864, ♂ a.; Graham Mountains, Ash Creek, June 15, 1914, ♂ a.; Huachuca Mountains, July 12, 1929, ♀ a.; Phoenix, Apr. 21, 1922, ♂ a.; Quitovaquito, Feb. 4, 1894, ♂ a.; Safford, July 25, 1914, ♂ jv.; San Bernardino Ranch, Mexican boundary line, Aug. 23, 1893, ♂ a.; Santa Cruz River, W of Patagonia Mountains, May 30, 1893, ♀ a., June 23, 1893, ♂ a., July 9, 1893, ♀ a.; San Pedro River, Mexican boundary line, July 30, 1893, ♂ jv.; Warsaw, Dec. 1, 1893, ♂ a.; Yuma County, 3 mi. east of Dome, May 26, 1918, ♂ a,; Yuma County, Wellton, May 31, 1918, ♂ a. ARKANSAS: Delight, May 15, 1914, ♂ a.; Stuttgart, May 1, 1953, ♂ a., May 6, 1953, ♂ a. CALIFORNIA: Baird, May 29, 1883, ♂ a., May 29, 1883, ♀ a. (not typical, dark); Del Monte, June 20, 1909, ♂ a.; Goffs, Apr. 11, 1905, ♂ a.; Laguna, San Diego County, June 15, 1894, ♀ a. (not typical, dark); Mountain Spring, San Diego County, May 15, 1894, ♀ a., May 15, 1894, ♂ a.; San Clemente Island, Aug. 26, 1894, ♂ a.; Saugus, Los Angeles County, May 16, 1931 [♂] a.; San Mateo County, June 5, 1899 [♂] a.; south of Yolla Bolly Mountain, July 28, 1905, ♂ jv. COLORADO: Empire, Clear Creek County, July 7, 1877, ♀ a.; Maybell, June 23, 1952, ♀ a. CONNECTICUT: New Haven, Aug. 4, 1900, ♂ a. FLORIDA: Norias Plantation, Jefferson County, Dec. 24, 1953, ♀ a.; North Jefferson County, Dec. 24, 1953, ♀ and ♂ a.; West Palm Beach, May 27, 1953, 3 ♂ jv. GEORGIA: Cairo, Grady County, Jan. 1, 1954, ♂ a.; southeast Thomas County, Mar. 25, 1954, ♂ a.; Sherwood Plantation, Grady County, July 21, 1953, ♂ a. IDAHO: Blackfoot, Bingham County, July 8, 1898, ♂ a., May 2, 1931, ♂ a.; Glenno Ferry, July 4, 1910, ♂ a.; Gray, May 29, 1952, ♂ a.; Hauser, Kootenai County, July 21, 1952, ♂ im.; Lewiston, July 12, 1952, ♀ a., Aug. 19, 1954, ♀ a., July 24, 1954, ♀ a., Aug. 21, 1954, ♀ a., Nov. 11, 1918, ♀ im., Dec. 13, 1948, ♀ a., Nov. 16, 1951, ♂ a., Oct. 14, 1951, ♀ a., Jan. 19, 1954, ♂ a., Dec. 28, 1951, ♂ im.; Montpelier, May 20, 1930, ♀ a., June 8, 1930, ♀ a., May 20, 1950, ♀ a., June 21, 1930, ♂ a.; Moscow, May 12, 1950, ♂ a., May 27, 1948, ♂ a., July 19, 1952, ♂ a., Aug. 26, 1954, ♂ jv., Dec. 28, 1950, ♀ im., Aug. 16, 1952, ♂ a.; New Meadows, Adams County, July 22, 1929, ♂ a. (not typical, dark), July 22, 1929, ♀ a.; 3 mi. southeast of Riddle, Owyhee County, July 2, 1932, ♂ a.; Potlatch, Sept. 5, 1954, ♀ jv., Oct. 18, 1953, ♂ jv.; Soda Springs, Caribou County, May 1, 1930, ♀ and ♂ a.; 1 mi. N of Spencer, Clark County, June 12, 1931, ♂ a.; Swan Lake, July 7, 1911, ♂ a. ILLINOIS: Beecher, Will County, Apr. 12, 1955, ♀ a., June 1, 1952, ♂ a., Sept. 12, 1955, ♂ a.; Genessee, Henry County, June 14, 1953, ♂ a.; Glenwood, Cook County, Aug. 2, 1953, ♂ a.; Grayville, White County, June 16, 1953, ♂ a.; Halíday, May 1, 1877, ♀ a.; Hissony, Fayette County, June 16, 1953, ♂ a.; Knoxville, June 15, 1953, 2 ♂ a.; Lacon, July 26, 1913, ♂ a.; Manteno, Will County, Sept. 12, 1954, ♀ a.; Noble, June 3, 1878, ♀ a.; Pana, June 15, 1953, ♂ a.; Ramsey, June 16, 1953, ♂ a.; 4 mi. south of Roseville, June 15, 1953, [♂] a.; West Liberty, Jasper County, June 16, 1953, ♂ a.; Wheaton, May 8, 1921, ♂ a.; White Oak, Montgomery County, June 15, 1953, [♂] a. INDIANA: Wheatland, May, 1885, [♀] a. IOWA: Charlotte, Clinton County, June 14, 1953, ♂ a.; Dallas Center, Dallas County, June 12, 1952, ♂ a.; Pleasantville, Marion County, June 13, 1953, ♂ a.; Prairie City, Jasper County, June 13, 1953, ♂ a.; Sioux City, June 12, 1953, ♂ a. KANSAS: Barber County, May 16, 1911, ♀ a., 10 mi. northwest of Cherryvale, June 9, 1953, 5 ♂ a.; Douglas County, Aug. 4, 1909, ♂ and ♀ a., Aug. 3, 1909, ♂ a.; Fort Hays, June 2, 1871, ♂ a.; Hamilton County, June 30, 1936, ♂ a.; Humboldt, Allen County, June 9, 1953, ♂ a.; 5 mi. west of Iola, Allen County, June 9, 1953, ♀ jv.; Labette County, July 19, 1915, ♂ a., July 21, 1915, ♂ a.; Lawrence, July 30, 1909, ♂ a., July 25, 1921, ♂ a., Sept. 28, 1907, ♂ a., Sept. 11, 1908, ♀ a., Nov. 2, 1907, ♀ a., Aug. 24, 1907, 2 ♂ a., Aug. 24, 1907, ♀ a.; Strong (near), July 15, 1891, ♂ a., July 21, 1891, ♂ a.; Nortonville, June 10, 1953, ♀ and ♂ a.; Okalusa, June 10, 1953, ♂ a.; Topeka, May 19, 1871, 3 ♂, 1 ♀ a., June 10, 1953, ♂ a.; Wallace, Wallace County, July 6, 1911, ♀ a. KENTUCKY: Rock Haven, Apr. 26, 1938, ♂ a. LOUISIANA: Arkana, June 3, 1953, ♂ a.; Morgan City, Nov. 1, 1925, ♀ im.; University, East Baton Rouge Parish, June 6, 1953, ♂ jv., Aug. 5, 1953, ♂ a. MAINE: Mount Desert Island, Teal Harbor, Aug. 12, 1902, ♂ a. MARYLAND: Chevy Chase, May 15, 1930, ♂ a.; Patuxent Research Refuge,

Laurel, Apr. 17, 1894, ♂a., Oct. 27, 1953, ♀im.; Whaleyville, Mar. 10, 1951, ♂a. MICHIGAN: Ann Arbor, May 13, 1941, ♂a.; Delhi, Washtenaw County, May 2, 1935, ♀a.; Kalamazoo, May 9, 1886, ♂a. MINNESOTA: Anoka County, July 22, 1940, ♂a.; Brainerd, July 9, 1954, ♂a.; Camden, May 14, 1946, ♂a.; Deerwood, July 12, 1897, ♂a.; Elk River, July 6, 1954, ♀a.; Fort Snelling, May 23, 1903, ♀a.; Hayfield, July 5, 1954, ♂a.; Hennepin County, June 26, 1948, ♂a.; Luverne, June 6, 1916, ♂a.; Madison, May 13, 1895, ♂a.; Minneapolis, May 16, 1892, ♀a., Aug. 30, 1890 [♂] and ♀a.; New Ulen, May 15, 1954, ♀a.; Princeton, July 7, 1954, ♂a.; Rochester, June 16, 1954, ♂a., June 19, 1954, ♂a.; St. Paul, June 17, 1954, ♀a.; Warren, Marshall County, June 14, 1928, ♂a. MISSOURI: Charleston, May 12, 1879, ♂a.; Gregory, Clark County, June 15, 1953, ♂a.; Kenmore, June 10, 1953, 2 ♂a.; Phelps City, June 11, 1953, ♂a.; Skidmore, June 10, 1953, ♂a. MONTANA: Billings, June 10, 1954, ♂a.; Crow Agency, Aug. 8, 1916, ♂a.; Gallatin Station, Sept. 8, 1888, ♂jv.; Glendive, July 15, 1954, ♀a., May 5, 1916, ♂a. (not typical, dark); Greycliff, July 16, 1954, ♂a.; Hilger (5 mi. NW), Aug. 4, 1919, ♀a. (not typical, dark); Livingston, June 9, 1954, ♂a.; Miles City, June 25, 1918, ♂a., July 15, 1954, ♂a.; Moorhead, June 21, 1916, ♀a. NEBRASKA: Auburn, June 11, 1953, ♂a.; Crete, Saline County, July 15, 1880, ♂a.; Dunbar, June 11, 1953, ♂a.; Johnson, June 11, 1953, ♀ and ♂a.; Louisville, June 11, 1953, ♂a.; Peru, June 11, 1953, ♂ and [♂] a.; South Sioux City, June 12, 1953, ♂a.; Springfield, June 11, 1953, ♂a.; Valentine, July 27, 1933, ♀a.; Brownsville (west of), June 11, 1953, ♂a. NEVADA: Carson City, Apr. 23, 1868, ♂a.; Head of Reese River, May 23, 1898, ♂a. NEW JERSEY: Cape May, Apr. 1842, ♀a. NEW MEXICO: Animas Mountains, Aug. 6, 1908, ♂a.; Corner Monument, 100 mi. west of El Paso, Apr. 24, 1892, ♂a., May 5, 1892, ♂a.; Dog Spring, Grant County, May 21, 1892, ♂ and ♀a.; La Mesilla, July 11, 1913, ♂a.; Las Cruces, July 22, 1913, ♂a.; Rinconada, May 1, 1904, ♂a.; Santa Fe, June 20, 1874, ♂jv. NORTH DAKOTA: Bismarck, July 13, 1954, ♀ and ♂a.; Drayton, June 18, 1915, ♂a.; Fargo, June 12, 1954, ♀a., July 12, 1954, 2 ♂a.; Grafton, May 9, 1912, ♂a.; Grassy Butte, July 14, 1954, 2 ♀a.; Lac Aux Morts, May 29, 1901, ♀a.; Turtle Lake, McLean County, July 9, 1925, [♂] a.; Wahpeton, June 9, 1915, ♂a.; Williston, July 14, 1954, 2 ♂a. OKLAHOMA: (Type specimen of *marginella*) In the cross timbers on north fork of Canadian River, Sept. 6, 1850, —jv.; Madill, Marshall County, July 26, 1954, 3 ♂a.; Minco, May 31, 1905, ♂a.; Morris, June 7, 1953, ♂a.; Muskogee, June 8, 1953, 2 ♂a., June 8, 1953, 2 ♂ and 1 ♀jv.; Pryor, June 8, 1953, ♂a.; Sayre, June 10, 1952, ♂a.; Willis, Marshall County, June 23, 1954, ♀a. OREGON: Adel, June 19, 1930, ♂a., June 3, 1930, ♀a., May 9, 1930, ♂a.; Hart Mountains, Lake County, June 22, 1928, 2 ♀a.; Nyssa, Malheur County, May 28, 1933, ♀a., May 23, 1933, ♂a.; Ordnance, July 31, 1954, ♀a., Nov. 20, 1954, ♂im.; Portland, May 18, 1933, ♂a., Aug. 9, 1924, ♀im.; Wallawa, Wallawa County, June 15, 1930, ♂a.; Wallawa Lake, Aug. 25, 1897, ♂a.; Wood Ranch, 5 mi. southwest of Ontario, May 16, 1916, ♂a. SOUTH CAROLINA: Christchurch Parish, May 11, 1911, ♂a. SOUTH DAKOTA: Custer, June 12, 1954, ♂ and ♀a.; Pierre, June 14, 1954, ♂a. TENNESSEE: Hickory, Apr. 20, 1937, ♀ and ♂a.; Hornbeak, May 4, 1937, ♀a.; Waynesboro, May 13, 1937, ♂a. TEXAS: Brownsville, Apr. 13, 1922, ♀a., June 2, 1924, ♂jv.; Cameron County, July 2, 1924, ♀jv.; Carterville, Cass County, June 4, 1954, ♂a.; Chinati Mountains, Presidio County, Aug. 5, 1887, ♀im.; Falfurias, Nov. 24, 1951, ♀a.; Fort Stockton, ———, [♀] a.; Leesburg, June 4, 1953, ♂a.; Linden, June 4, 1953, ♂a.; Menard County, June 6, 1952, 2 ♂a.; Killeen (11 mi. NW), Coryell County, July 23, 1950, ♀a.; Parker County, June 5, 1953, 2 ♂a.; San Elezario, Dec. 14, 1854, ♂a.; Tarrant County, June 6, 1953, 3 ♂a., ♂jv. UTAH: Farmington, May 17, 1911, ♂a.; Provo, July 25, 1872, ♀a., July 30, 1872, ♂a. VIRGINIA: Smith's Island, Sept. 7, 1895, ♂im. WASHINGTON: Clarkston, July 24, 1952, ♀a.; Fort Steilacoom, ———, [♂] a.; Grande Ronde River, June 14, 1919, ♀a.; Orting, Pierce County, May 28, 1954, 2 ♂, ♀a.; Palouse, Aug. 2, 1950, ♂jv.; Pullman, Sept. 28, 1954, ♂jv.; Renton, May 22, 1954, 2 ♂a.; Snake and Palouse rivers, May 22, 1860, ♂a.; Yelm, Thurston County, May 27, 1954, ♀ and ♂a. WISCONSIN: Babcock, June 25, 1954, ♂a.; Baldwin, June 29, 1954, ♂a.; Black River Falls, June 24, 1954, ♂a.; Camp Douglas, July 9, 1890, ♀a.; Durand, July 3, 1954, ♂a.; Ellsworth, June 30, 1954, ♀ and ♂a.; Milton, Apr. 19, 1896, ♂a.; New Lisbon, June 23, 1954, ♂jv.; Spooner, July 2, 1954, ♀a.; Turtle Lake, June 29, 1954, ♂a.; Wayerhauser, July 1, 1954, ♂a. WYOMING: Fort Bridger, July 4, 1858, ♂a.; Greybull, June 14, 1910, ♀a.; Wilson (10 mi. S), Teton County, July 30, 1947, ♀a. BAJA CALIFORNIA: La Paz, Feb. 17, 1882, ♀a.; San Nicholas, N of Cape San Lucas, Oct. 1859, ♀im. CHIAPAS: Cluapo, Ginetta Mountains, Jan. 25, 1869, ♂a. CHIHUAHUA: Colonia García, Feb. 25, 1904, ♀a. COLIMA: Plains of Colima, Jan. 1863, ♂a. GUERRERO: Amojileca, 20 km. W Chilpancingo (5800 ft.), Oct. 23, 1944, ♂jv.; Chilpancingo, Feb. 17,

1944, ♂ a. MICHOACÁN: Quiroga, north side of Lake Pátzcuaro (6800 ft.), Feb. 21, 1945, 2 ♂ a. MORELOS: Lake Rodeo, 5 km. east of Tetecala (4000 ft.), Jan. 27, 1945, ♂ a., Jan. 28, 1945, ♀ a. OAXACA: Tlacolula, 30 km. SE Oaxaca (5000 ft.), Sept. 7, 1947, ♀ im., ♀ and ♂ a.; Tamazulapan, 6 km. E (6600 ft.), Sept. 5, 1945, ♂ a. SAN LUIS POTOSÍ: Salinas, Aug. 2, 1947, ♀ a.; Labor del Río, Aug. 10, 1947, ♀ a.; Villa de Reyes, Laguna de las Rusias, Aug. 6, 1947, [♀] a.; Bledos, May 12, 1951, ♂ a. SONORA: Nogales, Oct. 25, 1893, [♂] a.; Hermosillo, May 6, 1892, ♂ a. VERACRUZ: Orizaba, ———, [♀] a.; Tres Zapotes, Mar. 11, 1939, ♂ a. GUATEMALA: Chimaltenango, Nov. 7, 1936, ♀ a.; Panajachel, May 2, 1946, ♀ a. NICARAGUA: Chinandega, ———, [♀] a.; Sucuya, ———, ♀ a. EL SALVADOR: ———, [♂] a. COSTA RICA: San Jose, ———, [♂] a.

Zenaidura macroura carolinensis

NEWFOUNDLAND: 1929, ♀ im.; Badger, Dec. 5, 1944 [♂] a.; Port aux Basques, Oct. 5, 1946, [♂] im.; Red Island, Dec. 2, 1946, [♀] im.; Rose Blanche, Oct. 22, 1946, ♂ im.; St. John's, Dec. 1945, [♀], im. ALABAMA: Auburn, June 25, 1936, ♀ a., July 1, 1936, ♀ a., June 26, 1936, ♀ a., Aug. 12, 1936, ♂ im. ARKANSAS: Stuttgart, May 24, 1953, ♂ a., June 16, 1953, ♂ a. DISTRICT OF COLUMBIA: Washington, Sept, 2, 1878, ♂ jv., June 9, 1875, ♂ a., April 12, 1888, ♂ a., April 21, 1874, ♂ a., April 5, 1910, ♂ a. FLORIDA: Big Lake George, Mar. 22, 1886, ♂ a.; Cape Sable, Mar. 27, 1926, ♂ a.; Gainesville, Jan. 1, 1930, [♂] a.; Glass, June 1, 1953, ♂ a.; Hialeah, Dade County, Oct. 28, 1948, ♀ im.; Homestead, May 30, 1953, ♀ jv.; Lake Harvey, Feb. 18, 1896, ♀ a.; Matanzas Inlet, May 22, 1894, ♂ a.; Miami, Nov. 24, 1904, ♀ im.; Overstreet, Feb. 9, 1920, ♂ a.; Sebring, Mar. 20, 1923, ♂ a.; West Palm Beach, May 27, 1953, 2 ♀ im., Aug. 8, 1956, 2 ♂, 4 ♀ a. GEORGIA: Milton County, Feb. 28, 1913, ♂ and ♀ a., Sept. 15, 1913, ♀ jv.; Roswell, Nov. 10, 1912, ♂ a., Nov. 5, 1915, ♀ im.; Sherwood Plantation, Grady County, July 22, 1953, ♂ a. IDAHO: Lewiston, Jan. 24, 1952, ♂ a. ILLINOIS: Fox Lake, May 26, 1905, ♂ a.; Genesee, July 16, 1897, ♀ a.; Glenwood, Jan. 1, 1955, ♀ a.; Oconee, June 16, 1953, ♂ jv. INDIANA: Richmond, July 25, 1896, ♂ a. IOWA: Charter Oak, June 12, 1953, ♂ a.; Des Moines, June 13, 1953, ♂ a.; Pleasantville, June 13, 1953, ♂ a.; Prairie City, June 13, 1953, ♂ a.; Yale, June 12, 1953, ♀ a. KANSAS: Garnett, June 9, 1953, ♀ a.; Strong, July 18, 1891, ♂ a. KENTUCKY: Canton, Oct. 29, 1938, ♂ a.; Hickman, May 31, 1938, ♀ a.; Madisonville, Oct. 20, 1938, ♀ im.; Montecello, June 15, 1938, ♂ a.; Rocky Branch, June 7, 1938, ♂ a. LOUISIANA: Alexandria, Mar. 19, 1953, ♂ a.; Bienville, July 18, 1933, [♂] a., ? jv.; Colfax, June 2, 1953, ♀ a.; Coushatta (3 mi. S), June 3, 1953, ♂ a.; Coushatta (8 mi. S), June 3, 1953, ♂ jv.; New Orleans, July 30, 1938, ♂ jv.; University, East Baton Rouge Parish, June 6, 1953, 2 ♀, ♂ a., June 11, 1953, ♂ im., Aug. 5, 1953, ♂ a. MARYLAND: Baltimore, Mar. 14, 1885, ♀ a.; Cornfield Harbor, July 17, 1894, ♂ a.; Halfway, Aug. 17, 1924, ♂ jv.; Laurel, Mar. 3, 1889, ♀ a., July 30, 1877, ♂ jv., May 3, 1889, ♂ a.; Laurel, Patuxent Research Refuge, Oct. 22, 1953, ♂ and ♀ a., Oct. 23, 1953, ♀ a., Oct. 27, 1953, 2 ♀ im., 3 ♂ im., ♂ a., Oct. 29, 1953, ♂ a.; Skaggsville, Howard County, Dec. 7, 1923, ♂ a.; Takoma Park, July 22, 1931, ♂ jv.; Washington County, June 19, 1953, ♀ jv. MASSACHUSETTS: Chathamport, Aug. 28, 1886, ♀ a.; Sherborn, May 26, 1885, ♀ a.; Taunton, May 26, 1908, ? jv.; Wareham, Aug. 10, 1882, ♀ a. MICHIGAN: Ann Arbor, May 29, 1954, ♂ a., Aug. 19, 1933, 2 ♀, ♂ a.; Pittsfield, Washtenaw County, May 27, 1928, ♂ a.; Portage Lake, Livingston County, May 8, 1935, ♂ a.; Clinton (9 mi. W), Washtenaw County, Aug. 13, 1935, ♀ and ♂ a., Aug. 23, 1935, ♂ a.; Waterloo, Sept. 12, 1922, ♂ jv., Nov. 7, 1920, ♀ a. MISSISSIPPI: Carriere, Aug. 12, 1919, ♂ a.; Rosedale, June 16, 1941, ♀ a.; June 14, 1952, ♂ a., June 1, 1952, ♂ a., Aug. 31, 1951, ♂ a. MISSOURI: Gregory, June 15, 1953, ♀ a.; St. Louis, May 8, 1857, ♀ a. NEW JERSEY: Camp Gaw, Franklin Lakes Borough, Nov. 10, 1930, ♂ im.; Lakehurst, June 1, 1924, ♂ a. NEW MEXICO: Big Hatchet Mountains, July 19, 1908, ♀ a.; Juarilla Mountains, Sept. 13, 1903, ♂ jv. NEW YORK: Cayuga Lake, May 4, 1913, ♂ a.; Long Beach, Aug. 12, 1919, ♂ a. NORTH CAROLINA: Asheville, Dec. 18, 1930, ♀ a., Jan. 30, 1934, ♂ a.; Engelhard, Oct. 17, 1939, ♀ im., Oct. 16, 1939, ♀ a.; Fort Macon, Apr. 24, 1869, ♂ a., July 6, 1915, ♂ a.; Rockingham, June 1, 1939, 2 ♂ a.; Smith Island, May 22, 1939, ♀ a. OHIO: Circleville, Nov. 26, 1880, ♀ a.; Cleveland, May, 1892, ♂ a.; East Claridon, May 19, 1937, ♀ a.; Ottawa County, Bay Point, June 8, 1937, ♀ a., June 24, 1935, ♀ a.; Pickerington, June 18, 1953, 2 ♂ a.; Rockport (Rocky River), ———, [♀] a.; Sandusky, May 10, 1946, ♂ a.; Shaker Heights, May 1, 1942, ♀ a.; Solon, June 29, 1944, ♂ a.; South Euclid, June 30, 1937, ♀ jv. OREGON: (Type specimen of *caurina*) [♂] im. PENNSYLVANIA: Carlisle, Sept. 20, 1943, ♂ a.; Chester County, Dec. 29, 1884, ♂ a.; Erie, Apr. 29, 1894, ♂ a. SOUTH CAROLINA: Chester, Sept. 26, 1940, ♂ jv.; Christchurch Parish, Apr. 29, 1911, ♂ and ♀ a., May 11, 1911, ♀ a.; Kershaw County, Dec. 27, 1904, ♂ a.; Lynch-

burg, Nov. 8, 1940, ♂ a., Nov. 8, 1940, 2 ♂ im.; McCormick, June 7, 1940, ♂ a., June 13, 1940, ♂ a. (not typical, pale). TENNESSEE: Nashville, May 19, 1945, ♂ a.; Pikeville, May 21, 1937, ♂ jv.; Tiptonville, Oct. 20, 1937, ♂ jv.; Waynesboro, May 12, 1937, ♀ a. TEXAS: Brownwood, Aug. 25, 1888, ♀ jv.; Citrus City, Hidalgo County, Oct. 12, 1952, 2 ♂ a.; Leesburg, June 4, 1953, ♀ a.; Pittsburg, June 4, 1953, ♂ a.; Tarrant County, June 6, 1953, ?jv. VERMONT: (northern), Sept. 4–5, 1905, ♂ jv. VIRGINIA: Cape Charles, Dec. 28, 1914, ♀ a.; Falls Church, Sept. 25, 1923, ♀ jv., Nov. 10, 1904, ♂ im.; Four Mile Run, Arlington County, July 22, 1894, ♀ im.; Mount Vernon, Oct. 21, 1892, ♂ a. WISCONSIN: Beaver Dam, Dodge County, May 12, 1899, ♀ a.; Lake Koshkonong, July 29, 1897, ♂ and ♀ a.; Madison, Aug. 22, 1949, ♂ a.; Platteville, June 27, 1889, ♂ a. GUERRERO: Ciruela (10 km. S Atoyac, 500 ft.), Dec. 11, 1944, ♀ a.; Polintla (6 mi. S Arcelia, 1600 ft.), Nov. 29, 1944, ♀ im. VERACRUZ: Mirador, Oct. ———, ♀ a.; Orizaba, ———, [♀] a.; Tres Zapotes, May 2, 1940, ♂ a. NAYARIT: (Type specimen of *tresmariae*) Tepic, Tres Marías Islands, May 5, 1892, ♂ a. GUATEMALA: 1877, [♀] a. NICARAGUA: Realejo, Feb. 7, 1864, ♀ a. BAHAMA ISLANDS: Long Island, July 16, 1903, ♂ a. HAITI: l'Atalage, Jan. 9, 1929, ♀ a.; Port au Prince, ———, ♀ a.

Zenaidura macroura carolinensis x *marginella*

NEWFOUNDLAND: Jan., 1947, ♂ a. ALABAMA: Auburn, July 13, 1936, ♂ jv., June 10, 1936, ♂ jv. ARIZONA: Warsaw Mills, Dec. 1, 1893, ♂ im. ARKANSAS: Delight, May 16, 1914, ♀ a.; Fayetteville, June 4, 1951, ♂ a.; near Bradley, U. S. Route 10, 5 mi. north of Louisiana line, June 3, 1953, ♂ and ♀ a.; Stuttgart, Sept. 28, 1951, ♀ im. CONNECTICUT: Woodbridge, New Haven County, May 12, 1900, ♀ a. DISTRICT OF COLUMBIA: Washington, Mar. 5, 1891, ♂ a. FLORIDA: Gainesville, Nov. 27, 1929, ♂ a.; West Palm Beach, May 27, 1953, ♀ a., ♂ jv. GEORGIA: Athens, Feb. 13, 1929, ♂ a.; Roswell, May 11, 1904, ♂ a. ILLINOIS: Beecher, Will County, June 15, 1952. ♂ a.; Crete, Will County, June 14, 1953, ♂ jv.; Fox Lake, Lake County, May 26, 1905, ♂ a. INDIANA: Wheatland, Jan. 19, 1888, ♀ a. IOWA: Castana, June 12, 1953, ♂ a. KANSAS: Cherokee County, June 23, 1915, ♀ a.; Douglas County, July 30, 1909, ♀ a.; Washington Creek, Douglas County, Aug. 2, 1909, ♀ a.; Garnett, June 9, 1953, ♀ a.; Lawrence, Sept. 11, 1908, ♀ a., Aug. 24, 1907, ♀ a.; Cherryvale (10 mi. NW), June 9, 1953, ♂ a.; Ozawkie, June 10, 1953, 3 ♂ a.; Strong, July 15, 1891, ♀ a.; Thompsonville, June 10, 1953, ♂ a.; Topeka, May 19, 1871, ♀ a.; Topeka (5 mi. NE), June 10, 1953, ♂ a. KENTUCKY: Madisonville, Oct. 21, 1938, ♂ a.; Waverly, May 16, 1938, ♂ a. LOUISIANA: Colfax (3 mi. N), June 2, 1953, ♂ a.; University, East Baton Rouge Parish, June 7, 1953, ♂ a., June 6, 1953, ♂ a., Aug. 5, 1953, ♂ a. MARYLAND: Swanton, July 19, 1899, ♀ jv.; Takoma Park, Feb. 5, 1946, ♀ a. MICHIGAN: Ann Arbor, May 4, 1904, ♂ a., July 31, 1937, ♂ a., June 14, 1942, ♂ a.; Powers, Jan. 5, 1923, [♂] a.; Rush Lake, Huron County, Aug. 4, 1908, ♀ a.; Sand Point, Huron County, July 14, 1908, ♀ a.; Wayne County, Apr. 20, 1909, ♀ a. MINNESOTA: Fort Snelling, May 15, 1903, ♀ a.; Kasson, June 19, 1954, ♀ a.; Mazeppa, June 20, 1954, ♀ a.; Minneapolis, July 26, 1932, ♂ a. MISSISSIPPI: Bay Saint Louis, Oct. 7, 1898, ♂ im. MISSOURI: Dothan, June 10, 1953, 2 ♂ a.; Maitland, June 10, 1953, ♂ a.; Quitman, June 10, 1953, ♂ a.; Skidmore, June 10, 1953, ♀ a. MONTANA: Glendive, July 15, 1954, ♀ a. NEBRASKA: Lorton, June 11, 1953, ♂ a.; Nickerson, June 11, 1953, [♀], ♀ a.; Orum, June 11, 1953, ♀ and ♂ a.; South Sioux City, June 12, 1953, 3 ♂ a. NEW YORK: Lawrence, Aug. 1, 1919, 2 ♂ im.; Montauk Point, Aug. 12, 1911, ♀ im. NORTH CAROLINA: Asheville, Jan. 20, 1934, ♂ a.; Southport, May 11, 1939, ♀ a. NORTH DAKOTA: Turtle Lake, July 9, 1925, ♂ a.; Valley City, May 22, 1912, ♂ a. OHIO: Bay Point, Ottawa County, June 8, 1937, ♀ a.; Guilford Lake, Columbiana County, June 13, 1939, ♂ a.; Mentor, May 27, 1937, ♀ jv.; Pickerington, June 18, 1953, ♂ a.; Union Township, Clermont County, July 25, 1940, ♂ a. OKLAHOMA: Fobb, Marshall County, July 23, 1954, ♂ im.; Lenapah, June 8, 1953, 2 ♂ a.; Muskogee, June 8, 1953, 4 ♂, ♀ a.; Pryor, June 8, 1953, ♀ a.; Yukon, June 7, 1953, 2 ♀ a. SOUTH CAROLINA: Beaufort County, May 1, 1941, ♂ a. TENNESSEE: Norris, June 11, 1938, ♂ a.; Rockwood, Apr. 8, 1884, ♂ a. TEXAS: Falfurias, Nov. 24, 1951, ♂ im.; Johnson County, June 5, 1953, ♀ and ♂ a.; Leesburg, June 4, 1953, ♂ a.; Parker County, June 5, 1953, 2 ♂ a.; Premont, Nov. 22, 1951, ♀ jv., ♀ im.; Tarrant County, June 6, 1953, [♂], ♂ a., ♀ jv. VIRGINIA: Falls Church, May 17, 1938, ♂ a. WISCONSIN: Beaver Dam, Dodge County, May 27, 1900, ♂ a., May 12, 1899, ♂ a.; Lake Koshkonong, Aug. 5, 1897, ♂ and ♀ a., July 29, 1897, ♂ a. CHIHUAHUA: Casas Grandes, May 31, 1899, ♂ jv. VERACRUZ: Orizaba, —, [♀] a. CUBA: Las Villes Placetas, Feb. 27, 1948, ♂ a. COSTA RICA: Liberia, Nov. 1, 1940, ♂ a.; San Jose, —, ♂ a.

Zenaidura macroura macroura

FLORIDA: Plantation Key, May 29, 1953, 2 ♂, ♀a. CUBA: [♀] im., [♂] a.; N Sophie, Jan. 28, 1861, ♂a. STATE OF CAMAGUEY: Jababo, May 1, 1930, ♂a.; Minas, Mar. 7, 1948, ♂a.; Rabchardo Cay, Sept. 5, 1930, ♂a., ♂im. STATE OF HAVANA: Havana, Jan. 11, 1927, ♀a.; Laguna Ariguanabo, Apr. 21, 1920, ♂a. ISLE OF PINES: Sept. 26, 1930, [♂], ♀a.; Nueva Gerona, July 2, 1900, ♂jv., July 5, 1900, ♂ and ♀a., July 7, 1900, ♂a.; Santa Fe, Apr. 2, 1948, ♂a. STATE OF MATANZAS: Bolandran, Feb. 9, 1949, ♂a.; Matanzas (9 mi. NW), Feb. 11, 1949, 2 ♂a.; Perico, Feb. 10, 1949, ♂a. STATE OF ORIENTE: El Guamo, Feb. 27, 1900, [♀], [♂] a., Mar. 25, 1900, ♂ and ♀a., Nov. 30, 1901, ♂a., Jan. 22, 1949, ♂a., Dec. 31, 1901, ♀a.; Guantánamo, San Carlos Estada, Apr. 1, 1915, [♀], ♀a., Feb. 18, 1915, ♂a., Feb. 15, 1913, ♀a., Sept. 22, 1917, ♀im., ? jv., Feb. 9, 1914, ♀ and ♂a., Sept. 12, 1915, ♂a., Oct. 31, 1914, ♂a., Aug. 4, 1918, ♀im., Sept. 15, 1918, 2 ? jv., Sept. 17, 1915, ♀im., Aug. 7, 1915, ♂jv.; Holguin, Mar. 6, 1948, ♂a.; Port Gibara, Feb. 22, 1930, ♂a. STATE OF PINAR DEL RIO: Consolacion del Sur, Feb. 1, 1949, ♂a.; Guanajay, May 1, 1900, ♀a.; Mariel, May 10, 1900, ♀jv., (type specimen of *bella*) May 9, 1900, 2 ♂a.; Vinales, Feb. 1, 1949, ♀ and ♂a. STATE OF SANTA CLARA: Cumbre, Feb. 11, 1949, ♂a. HAITI: Bombardopolis (NW), Mar. 21, 1917, ♀a.; Fort Liberty, Feb. 15, 1929, ♂a.; La Gonave, En Cafe, Mar. 5, 1929, ♂a.; Moustique, Mar. 10, 1917, ♂a., May 4, 1917, ♀a.; Port au Prince, Mar. 28, 1930, ♂a.; St. Marc, Feb. 25, 1929, ♂a.; St. Michel, Jan. 6, 1929, ♂a.; Thomazeau, May 22, 1931, 4 ♀, ♂a.; Tortuga Island, Jan. 30, 1917, ♂a., May 18, 1917, ♂a., Jan. 31, 1917, ♂a. DOMINICAN REPUBLIC: Constanza, Sept. 28, 1916, ♂jv., May 1, 1919, ♀a., Sept. 22, 1916, ♂a., Oct. 1, 1916, ♂im.; Yaque River near Mount Cristi, June 22, 1927, ♂a.

Zenaidura macroura turturilla

GUATEMALA: Dept. de Santa Rosa, Cerritos, Mar. 27, 1946, ♀a. NICARAGUA: Chinandega, —, [♀] a. REPUBLIC OF PANAMÁ: COCLE PROVINCE: Anton, May 16, 1953, ♀a. (type specimen of *turturilla*). PANAMA PROVINCE: El Espino, Apr. 1, 1951, ♂a. VERAGUAS PROVINCE: San Francisco, Mar. 12, 1931, ♂a.; Sona, May 20, 1953, ♂a., June 5, 1953, ♂a, —, [♂] a.

Zenaidura macroura clarionensis

NAYARIT: (Type specimen of *clarionensis*) Clarión Island, Mar. 4, 1889, 3 ♂, 2 ♀a., Mar. 4, 1889, ♀im., Apr. 28, 1925, ♂a., Apr. 27, 1925, ♀a.

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CLASSIFICATION AND SYSTEMATIC POSITION OF THE EIDERS

By PHILIP S. HUMPHREY

This paper deals with part of the results of research (Humphrey, MS) on the Mergini, a tribe proposed by Delacour and Mayr in 1945 to include the Old-squaw, Harlequin, and Labrador ducks, and the mergansers, golden-eyes, scoters, and eiders. I shall deal here solely with the relationships and systematic position of the eiders, which my evidence indicates do not belong in the Mergini. Delacour and Mayr's conclusions regarding the close relationship of the golden-eyes and mergansers will be discussed elsewhere.

These studies were aided by a contract between the ONR, Department of the Navy, and the Arctic Institute of North America. Part of this work was undertaken with the assistance of a Rufus B. Kellogg Fellowship from Amherst College. I am deeply grateful for the support of these institutions. I am very much indebted to the many people who have given me advice and assistance, to the several museums which have loaned me specimens, and to the University of Michigan Museum of Zoology and Zoology Department for use of their facilities. Lastly, I am particularly indebted to the late Professor Josselyn Van Tyne, who was a constant source of encouragement and patient assistance.

The eiders, because of their lobed hallux and their habit of diving, have long been grouped with other ducks having those attributes. Hence, in most classifications, the eiders, pochards, scoters, steamer ducks, golden-eyes, and others have been placed together. In 1945, Delacour and Mayr erected the Tribe Aythyini exclusively for the pochards and put the eiders, along with the scoters, golden-eyes, mergansers, Old-squaw, Harlequin Duck, and Labrador Duck, in the Tribe Mergini. They state (*op. cit.*: 32) that "in spite of the wide difference between the extreme forms of the tribe (*Mergus* and *Somateria*), the sea ducks [Mergini] form one of the most closely knit subdivisions of the anatine subfamily."

It is clear from Delacour and Mayr's classification that ducks having the diving habit (and the lobed hallux) are not necessarily closely related. Nonetheless, the classical separation of "diving ducks" from "dabbling ducks" remains essentially unaltered in theirs and in most other recent classifications of the waterfowl.

Although the food habits and locomotor adaptations (including many correlated structural modifications) of the eiders are most like those of the scoters, those two groups of species have little else in common. In fact, the eiders as a group appear to share more characters with the "dabbling ducks" (Anatini) than with any other waterfowl.

Trachea.—Various authors, notably the Heinroths (1928) and Delacour and Mayr (1945), have commented on the value of the trachea as a source of evidence for the classification of ducks. A close examination of this structure in the Mergini suggests a taxonomic arrangement different from that proposed by Delacour and Mayr.

The tracheal bulla of each of the species of eiders has an inflated left chamber which is bulbous in form and lacks membrane-covered fenestrae (see figs. 1*a*, 1*b*, 1*c*, and 1*d*). The tracheas of the eiders lack mid-tracheal swellings and are (except for *Polysticta*) of uniform diameter (see fig. 1*a*). If I depended on tracheal characters alone, I would unhesitatingly place the eiders in Delacour and Mayr's Tribe Anatini. The tracheas and tracheal bullas of males of most members (the tracheas of several species are unknown) of the genus *Anas* (*sensu latu*) are very similar to those of the eiders, differing from them only in minor variations of shape.

The tracheas and tracheal bullas of members of the Tribe Mergini other than the eiders may be described as follows:

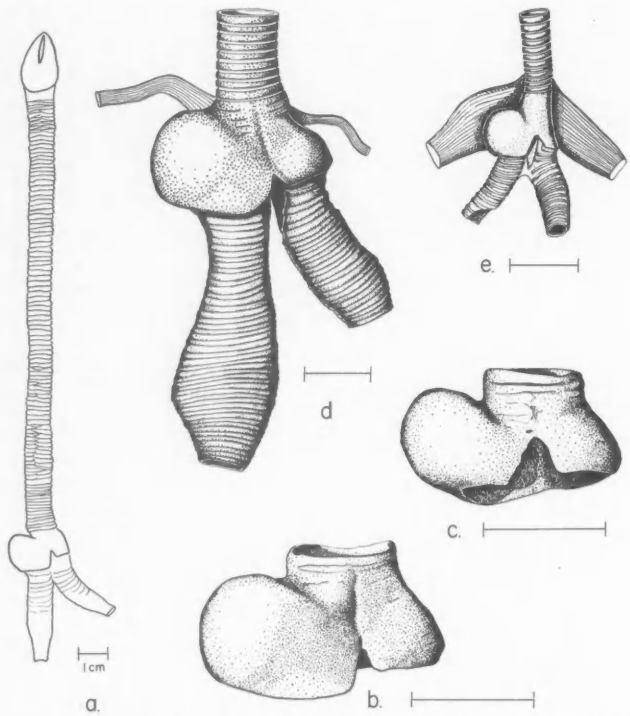

Fig. 1. Dorsal views of trachea and tracheal bullas of male eiders. *a*, trachea of *Somateria spectabilis*; *b*, tracheal bulla of *S. spectabilis*; *c*, tracheal bulla of *S. fischeri*; *d*, tracheal bulla and bronchi of *S. mollissima v. nigra* (note slender sternotrachealis muscles and enlarged left bronchus); *e*, tracheal bulla and bronchi of *Polysticta stelleri* (note enlarged sternotrachealis muscles and bronchi of equal size).

1. *Melanitta nigra*.—Males lack a tracheal bulla and have instead a small, fused (or partially fused), bilaterally symmetrical structure at the lower end of the trachea. This structure is similar to the structure at the lower end of the trachea of females. The tracheal tube is of uniform diameter. For figures see Yarrell (1845:321), Miller (1926:2), and Pycraft (1910:403).

2. *Melanitta fusca* and *M. perspicillata*.—The tracheal bulla of males of these two species is bilaterally symmetrical. The right and left chambers are enlarged and their lateral margins are dorso-ventrally compressed. Neither chamber has a bulbous appearance. The tracheal tube of each of these two species has a prominent mid-tracheal swelling in addition to an odd swelling in the laryngeal region. For figures see Miller (1926: 2) who illustrated the tracheas of *M. perspicillata* and *M. fusca*; also for figures of tracheas of *M. fusca* see Yarrell (1845:315–316), Latham and Romsey (1798: table 15, figs. 3–7), and Pycraft (1910:403).

3. *Clangula, Bucephala, Mergus* (including *Mergellus* and *Lophodytes*).—The tracheal bulla in males of species in these three genera is asymmetrical and consists of

two irregular inflations, at least one of which has one or two membrane-covered fenestrae. There is considerable interspecific variation in the superficial appearance of this type of tracheal bulla, although the basic structures are present in all the species having it. The right chamber may be only slightly inflated or it may be greatly inflated. The amount of fusion of the right chamber is also variable; in some the basic ring structure is easily discernible, while in others fusion is so complete that no rings can be traced at all. The left chamber is also variable. It always has at least one membrane-covered fenestra and fusion is generally so complete that ring outlines are indiscernible. The tracheal tubes of males of the several species of *Clangula, Bucephala* (except *B. albeola*), and *Mergus* have swellings, some of which are highly specialized bulbous structures and others merely slight increases in the diameter of the tube.

For figures of the trachea of *C. hyemalis* see Yarrell (1845:361–362), Montagu (1831:515), Sabine (1819: table 30, figs. 3 and 4), and Ruppell (1933:477). There is no readily available published figure of the trachea of *B. albeola* although a trachea of a male of that species is figured by Humphrey (MS). There are many figures of the trachea of *B. clangula* and *B. islandica*; the tracheas of both species are figured by Taverner (1919:58), Gilpin (1878:398–399), and Kortright (1942:261). The trachea of *M. albellus* was figured by Harrison (1943: pl. 7, fig. 1), Yarrell (1843:281), and Latham and Romsey (1798: table 16, figs. 3 and 4). Beard (1951:300) illustrated the trachea of *M. cucullatus*. For figures of the trachea of *M. merganser* see Eyton (1836: 76), Yarrell (1827: table 15; 1845:399), and Pycraft (1910:403). The trachea of *M. serrator* has been figured by Yarrell (1845:394), Latham and Romsey (1798: table 16, figs. 1 and 2), and Newton (1861:420). The tracheas of *M. australis, M. squamatus,* and *M. octosetaceus* are figured by Humphrey (MS).

The eiders (characterized by tracheas which lack swellings and which have bullas which are inflated to the left, bulbous in form, and lacking membrane-covered fenestrae) cannot be easily placed with *Clangula, Melanitta, Bucephala,* and *Mergus* on the basis of the structures of the trachea and the tracheal bulla.

The tracheal bullas of *Somateria mollissima* (fig. 1*d*), *S. spectabilis* (fig. 1*b*), and *Lampronetta* (formerly *Arctonetta,* see Parkes, 1955:85–86) *fischeri* (fig. 1*c*) are practically identical in form; they differ from one another only in size. *Somateria mollissima v. nigra* (fig. 1*d*) has the largest tracheal bulla and *Lampronetta fischeri* the smallest; the tracheal bulla of *Somateria spectabilis* is intermediate in size. The tracheal bullas of other races of *Somateria mollissima* are smaller than that of *S. m. v. nigra* but they are slightly larger than that of *Somateria spectabilis*. The left chamber of the tracheal bulla of each of the above three species is expanded mostly laterally; it is expanded slightly in an anterior direction; medially and ventrally the left chamber bulges in a ventral direction. The pessulus is a thin, vertical bar of bone; it is located anteriorly, close to the tracheal aperture of the bulla.

The tracheal bulla of *Polysticta stelleri* (fig. 1*e*) is smaller than those of *Somateria* and *Lampronetta* and differs from them as follows:

1. The left chamber is proportionately less expanded.

2. The left chamber has a prominent ventral protuberance at the posterior ventral margin of the bulla between the bronchial apertures.

3. The pessulus is wide (antero-posteriorly) in *Polysticta*; it is very narrow in *Somateria* and *Lampronetta*.

4. The shape of the left chamber in *Polysticta* differs from that of *Somateria* and *Lampronetta*.

The tracheas of all the eiders except *Polysticta* are of uniform diameter. The trachea of *Polysticta* gradually increases in diameter for the anterior quarter of its length.

The bronchi of all the eiders except *Polysticta* are enlarged, the left one more so than the right. The bronchi of *Polysticta* are not enlarged and are of equal size (figs. 1*d* and 1*e*). The bronchi of all the eiders are very close to one another anteriorly. Males of *Polysticta* are unique among the eiders in having very much enlarged sternotrachealis muscles (compare figs. 1*d* and 1*e*).

Plumage patterns.—On the basis of the plumage patterns of adult and immature females and downy young, Delacour and Mayr's Tribe Mergini can be divided into two groups: (1) the eiders, and (2) the scoters, Old-squaw, golden-eyes, Harlequin, and mergansers.

The eiders are at once distinguished from the other members of the Mergini by the barred, somewhat *Anas*-like pattern of the females. Females of the rest of the Mergini are either more or less uniform sooty brown with various head markings (*Melanitta, Histrionicus*) or they are contrasting, that is, having a brown head with or without markings, and a gray back contrasting with the light, unmarked belly (*Bucephala, Mergus, Clangula*).

The patterns of the downy young of the various species of Mergini fall into two main groups—the eiders in one and the rest of the species in the other. Downy eiders are brown and, except for *Polysticta,* all of them are quite pale. None of them has the bold pattern characteritstic of the golden-eyes, mergansers, scoters, Harlequin, and Old-squaw. All of the downy Mergini except the eiders are either slaty-brown or almost black. The face pattern of the downy eiders consists of a faint, pale superciliary and a fine, dark line through the eye; the other downy Mergini have a light cheek-patch, usually white but entirely or in part reddish-brown in most of the mergansers, contrasting with the dark crown. This cheek-patch is clearly apparent in *Melanitta nigra* and *M. perspicillata,* both of which lack the contrasting body markings of the mergansers, golden-eyes, and others.

Except for the head, the plumage patterns of downy young eiders are practically identical. All have light under parts and darker upper parts. The under parts vary from pale tan to pale grayish brown. Dorsally, the plumage varies from light brown to dark reddish brown and is unrelieved by any light markings. All except *Polysticta stelleri* have a prominent, pale superciliary; *Polysticta* has a narrow, light brown superciliary which does not extend anteriorly to the base of the bill.

Food habits.—I have observed adult Spectacled and Pacific eiders on the nesting grounds in Igiak Bay, Alaska, tipping up for plant food; my few observations lead me to suspect that eiders may take large percentages of plant foods while on the breeding grounds. Eiders take predominantly animal foods when away from the breeding grounds. Unfortunately, there are too few data from adult birds taken on the breeding grounds to describe their feeding habits in that season.

Cottam (1939:93, 104, 113) has described the stomach contents of downy young eiders as follows: *Polysticta stelleri* about 40 per cent plant food, *Somateria mollissima v. nigra* about 70 per cent plant food, and *Lampronetta fischeri* about 45 per cent plant food. The diets of downy young of the scoters, Old-squaw, golden-eyes, and Bufflehead contained no more than 25 per cent plant material (Cottam, *op. cit.*).

The winter (or marine) diets of the eiders (except *Polysticta*) are very similar to those of the scoters (see Phillips, 1926; Madsen, 1954; Cottam, 1939). The winter diet of *Polysticta* seems to be roughly similar to that of *Clangula.*

Diving habits.—Very little is known of the eiders' method of underwater locomotion. There is general agreement that the eiders use their half-spread wings in diving; no one, however, has determined whether or not they use their feet underwater. Bent (1925:89) states that "in diving the wings are partially opened and used to a limited

extent in swimming under water, but the wings are not wholly spread; progress seems to be made mainly by the use of the feet, and there is nothing like the full subaqueous flight practiced by some of the Alcidae." Phillips (*op. cit.*:91) says "there is no question but that Eiders use their wings under water, whether or not they are wounded . . . The Eider uses its wings just as does the Harlequin, held close to the sides and beaten with short jerks, not extended as in aerial flight." My own observations, and those of Frank McKinney (*in litt.*), are in agreement with Phillips' remarks.

When feeding in shallow water on the breeding grounds, eiders tip up like dabbling ducks. I have observed this behavior many times in *Somateria mollissima v. nigra* and *Lampronetta fischeri*; it is probably also a habit of *Somateria spectabilis* and *Polysticta stelleri*.

Genera.—Delacour and Mayr (1945:33) place the four species of eiders in the genus *Somateria* on the ground that differences in plumage patterns and bill shape do not constitute valid generic criteria. I agree with those authors that *Lampronetta* should be placed in *Somateria* for the following reasons:

1. The structure of the trachea and tracheal bulla of *Lampronetta* is practically indistinguishable from that of *Somateria* (see figs. 1*b*, 1*c*, and 1*d*).

2. The plumage pattern of downy young *Lampronetta* differs from that of *Somateria* only in a slight modification of the pattern around the eye.

3. The differences between the plumage patterns of adult male *Lampronetta* and *Somateria* are principally ones of distribution of black on the ventral parts and of pattern on the head; in most other particulars the plumage patterns are very similar.

4. The plumage patterns of the females are very similar, the major peculiarity of *Lampronetta* being the modified pattern around the eye.

5. The skeletal proportions of *Lampronetta* and *Somateria* are very similar.

6. One adult male specimen of *Lampronetta* (Colorado Museum of Natural History No. 8663) has the black gular "V" characteristic of *Somateria spectabilis* and *Somateria mollissima v. nigra*. This V-shaped throat marking has appeared frequently in races of *Somateria mollissima* other than *v. nigra*. Its occurrence suggests that all the forms in which it appears are closely related.

On the other hand, I consider that *Polysticta* should not be merged with *Somateria* for the following reasons:

1. The structure of the tracheal bulla and the associated sternotrachealis muscles of *Polysticta* differ from those of *Somateria* (see figs. 1*b*, 1*c*, 1*d*, and 1*e*).

2. The plumage patterns of adult *Polysticta* are very different from those of *Somateria*. The presence of a speculum in both sexes of *Polysticta* sets that species apart from the species of *Somateria*.

3. The skeletal proportions of *Polysticta* are strikingly different from those of *Somateria*.

4. The bill of *Polysticta* is entirely different from that of *Somateria*. The differences exhibited by the bill of *Polysticta* are not merely exaggerations or modifications of characteristics present in the bills of *Somateria*. The presence of soft skin along the distal half of the "cutting edge" of the upper mandible, and the absence of a well-defined nail not only distinguish *Polysticta* from *Somateria* structurally but also suggest that the species has a method of feeding quite different from that of *Somateria*.

5. In flight *Polysticta* has none of the attributes of the large eiders. *Polysticta* is not only swifter on the wing than any of the species of *Somateria* but it is also much more maneuverable. The flight of Steller's Eider is comparable in speed and maneuverability to that of the Old-squaw; I have seen both species flying together in a small, loose flock.

Systematic position of the eiders.—The structure of the trachea and tracheal bulla

and the plumage patterns of adult and young eiders lead me to believe that these birds are not closely related to the scoters, golden-eyes, and mergansers. In structure, the trachea and tracheal bulla of the eiders and the dabbling ducks (Anatini) are very similar; likewise, the plumage patterns of the females of both groups have much in common. I believe that the eiders are much more closely related to the dabbling ducks than they are to the scoters, golden-eyes, and mergansers. The diets of downy eiders consist of from 40 to 70 per cent plant food; presumably the adults on the breeding grounds also consume a great deal of plant material. Although much more information is needed on the diets of the eiders on their breeding grounds, my observations suggest that their summer feeding habits resemble those of the dabbling ducks, which depend largely on plant food. Furthermore, the eiders' method of feeding in shallow water on the breeding grounds (tipping up) is very similar to that of the dabbling ducks.

The eiders probably developed from a group of dabbling ducks (Anatini) that invaded the marine coastal habitat. There, the ancestral eiders presumably developed feeding habits in which animal material played an increasingly important role. Development of the diving adaptation enabled these birds to utilize food resources in deeper water. Most dabbling ducks dive occasionally; in diving, they use their half-opened wings as the means of underwater propulsion. The marine coastal nesting distribution of the eiders and their dependence on the wings as an important means of underwater locomotion lead me to think that they underwent the early stage of their adaptive evolution in that environment.

Delacour's (1956:17) suggestion that the eiders be placed in a separate tribe, the Somateriini, next to the Anatini, seems to me the most satisfactory arrangement.

SUMMARY

The tracheal structure, plumage patterns, food habits, and diving habits of the genera in the Tribe Mergini (Delacour and Mayr, 1945) are compared.

It is concluded that the eider genus *Lampronetta* should be placed in the genus *Somateria*, but that *Polysticta* should be maintained as a separate genus.

It is further concluded that the eiders have their closest relationships with the Anatini, and that they should be placed in a separate Tribe Somateriini, next to the Anatini, as proposed by Delacour (1956).

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Department of Vertebrate Zoology, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, July 24, 1957.

FROM FIELD AND STUDY

Further Records from the Pleistocene of Newport Bay Mesa, California.—Since my previous reports (Howard, Condor, 51, 1949:20–28, and 57, 1955:136) concerning fossil birds recovered from the Pleistocene marine deposits of the Newport Bay mesa, California, several more bones have been acquired from this area by the Los Angeles County Museum. Most of the specimens were taken on the east side of the estuary at locality number 1066, the main locality of the Los Angeles County Museum for vertebrate material in this area; three specimens were taken at the north end of the estuary at invertebrate localities numbers 136 and 240. Seven of the previously recorded species from the Newport Pleistocene are represented plus two more that have not previously been recorded as fossil. That the records may be kept up-to-date for this important region, the identifiable specimens are listed here. Those from localities 136 and 240 are so indicated; the others are from locality 1066.

Gavia stellata. Red-throated Loon. A complete ulna (no. 2423). This is the first fossil record of this species.

Gavia immer. Common Loon. A nearly complete tarsometatarsus (no. 2608 from loc. 240). An incomplete coracoid (no. 2421 from loc. 136) is large enough for *G. immer*, but the glenoid facet is shorter and broader than in available Recent specimens of this species.

Aechmophorus occidentalis? Western Grebe. A poorly preserved proximal end of a humerus (no. 2610).

Diomedea albatrus. Short-tailed Albatross. A complete tarsometatarsus (no. 2617).

Puffinus griseus. Sooty Shearwater. A distal end of a humerus (no. 2621). Another distal end of a humerus (no. 2622) may also belong to *P. griseus*. It is similar in size and in the deep, laterally compressed shaft, but the distal contours are incomplete, and the brachial area, although poorly preserved, appears somewhat less depressed. The specimen may be significant as it is more highly mineralized than is usual for the Pleistocene bones from Newport Bay and thus may represent a secondary deposition from older beds.

Phalacrocorax penicillatus. Brandt Cormorant. One scapula (no. 2611).

Anser albifrons? White-fronted Goose. An eroded distal end of an ulna (no. 2419). A fragment of a carpometacarpus (no. 2615) appears also to be that of a goose, but it is impossible to determine the species.

Chendytes lawi. Three femora (nos. 2606, 2619, 2620) and a tarsometatarsus (no. 2618) of this extinct diving goose are present. Femur no. 2606 is from locality number 136.

Catoptrophorus inornatus. Willet. A nearly complete humerus (no. 2058). This is the first fossil record of the Willet.

In addition to the foregoing, an incomplete carpometacarpus of the Pliocene species, *Mancalla californiensis* (no. 2583) was recovered from the typical Pleistocene strata, in locality no. 1066. The bone is more highly mineralized than those typical of the Newport beds and of a dark, warm brown color. The preservation closely resembles that of specimens of the same species taken from the nearby Pliocene deposits of Corona del Mar. It is suggested, therefore, that it may have been secondarily deposited from older sediments.

The Los Angeles County Museum is indebted to Mr. Fred Feltham, Mr. F. L. Grouard, Mrs. Eleanor McLauchlan, and Mr. and Mrs. Robert Zava for the recovery of eleven of the specimens here listed; the other five were collected by the Museum's curators of paleontology, Dr. Theodore Downs and Mr. George P. Kanakoff.—HILDEGARDE HOWARD, *Los Angeles County Museum, Los Angeles, California, August 26, 1957*.

Notes on the Red Crossbill in Nevada.—In recent years, the author has obtained records of the Red Crossbill (*Loxia curvirostra*) from several mountain ranges in Nevada which add to the fragmentary knowledge concerning the occurrence of this species in the state. Despite persistent field work in western Nevada from 1948 through 1954, crossbills were not detected until March 26, 1953, when two were observed feeding in the tops of piñons at Geiger Summit, 6800 feet, Virginia Range, Washoe County. On August 14, 1954, John S. Spencer and the author found flocks totaling approximately 30 birds in a mature lodgepole pine and white pine forest at Big Meadows, 8700 feet, two miles west of Hunter Lake in the Carson Range, Washoe County. One group of about 15 birds had

at least two lodgepole pines established as feeding trees, one at the edge of the meadow and the other one quarter of a mile distant into the forest. Apparently the crossbills periodically circulated between these points, for by waiting at the latter tree, a total of nine birds was collected at intervals through the afternoon. Crossbills had fed considerably in the two trees, perhaps for several days prior to our visit, as evidenced by the number of freshly emptied cones which littered the ground. On a return visit to the area on August 28, 1954, approximately 15 crossbills were found and a single streaked male was obtained.

According to the plumage sequence as outlined by Tordoff for this species (Condor, 54, 1952: 200–203; Condor, 56, 1954:108–109), the six males from Big Meadows may be segregated as follows: four in varying stages from start to completion of the postjuvenal molt, in each instance by the replacement of streaked juvenal feathers with xanthochroistic body plumage (left testis lengths of 1, 1, 1.5, and 3 mm.), one extremely worn red male which is a first-year bird in that it retains the greenish-edged rectrices of the juvenal plumage (testis 4 mm.), and a fully adult red male (testis 6 mm.). It is interesting here to note the apparent correlation between testis length and presumed age as based on plumage characters. Of the four females, two were undergoing the postjuvenal molt and had inactive gonads, one had nearly completed this molt and is in unworn first-year plumage, and one individual is an extremely worn adult. The latter two birds had enlarged ova.

As a group, the ten specimens (University of Nevada Museum of Biology collection) have been assigned to the race *grinnelli* on the basis of general coloration, length of exposed culmen, and wing length, although in the latter character as well as in overall bill mass an approach toward the smaller *bendirei* type is evident. One first-year female is too small for typical *grinnelli* (wing 85.5, culmen 16.3 mm.) and falls well within the range of *bendirei*. The small size of this individual might be due to age, for the findings of Tordoff (1952, *op. cit.*:202) indicate that with regard to wing length and bill measurements first-year birds are significantly smaller than adults, at least in the race *benti*. On the other hand, Jollie (Condor, 55, 1953:195) found that the mean measurements for these two age groups were the same in a series of *bendirei* from Idaho.

On June 11, 1957, between 7800 and 8200 feet on the north slope of Mount Magruder at two and one-half miles east of Indian Spring, Esmeralda County, small groups totaling approximately 20 birds were found generally distributed through the dense piñon groves. Many of the larger trees were heavily laden with cones and the crossbills were seen actively eating the piñon nuts. Two adult males (testis 4 and 5 mm.) and two streaked juveniles were obtained which represent the race *grinnelli* (Museum of Vertebrate Zoology nos. 135378–81). This record supplements the two earlier reports of the species from southwestern Nevada: Grapevine Mountains (Miller, Ecology, 27, 1946:56) and Indian Creek, White Mountains (Miller and Russell, Condor, 58, 1956:76–77). Crossbills have not often been recorded as presumed breeding birds from the piñon zone; it remains uncertain whether the species utilizes this plant formation in years of low cone production.

An additional locality record is provided by the observation, on June 14, 1957, of a small group of crossbills calling distinctively in flight over the old-growth piñon at 7300 feet, Sweetwater Canyon, Sweetwater Range, southern Lyon County.

In northeastern Nevada, the species has been reported once since 1868 (Gullion, Condor, 59, 1957:71). Recent field investigations by parties from the Museum of Vertebrate Zoology have provided specimen records of the Red Crossbill from Elko County. On June 22, 1955, Alden H. Miller collected a male (testis 3 mm.) and a female (largest ovum .5 mm.) at two miles northeast of Jarbidge Peak, elevation 9000 feet. The following day another female was taken at the same place. The author has allocated these specimens to the race *benti* (Museum of Vertebrate Zoology nos. 133313–15). The females in particular show the characteristic brightness of the ventral yellow, the whitish belly, and the long slender bill of this race. The male is xanthochroistic and rather dusky below, suggesting a degree of intermediacy toward *bendirei*. Despite the collection dates, the birds showed heavy fat and perhaps were post-breeding vagrants. Another male (Museum of Vertebrate Zoology no. 134440) with a testis length of three millimeters, taken by Ward C. Russell on the east slope of Spruce Mountain, 8400 feet, on June 26, 1956, appears to be an intergrade between *benti* and *bendirei* both in color and size (wing 91.5, culmen 18.3, bill depth 9.6 mm.).

A Red Crossbill was found dead by John S. Spencer on a dirt road at 5100 feet, three miles south and one mile west of Centerville, Douglas County, on December 4, 1956. The author salvaged the

bird as a study skin and identified it as *L. c. benti* (Museum of Vertebrate Zoology no. 135382). This identification was confirmed by A. H. Miller who examined the specimen later. There appear to be no other published records of this race from Nevada, although Linsdale mentions an individual obtained on the Arizona side of Lake Mead, November 14, 1938 (Condor, 53, 1951:245).

In his discussion of the race *grinnelli* in Nevada, Griscom (Proc. Boston Soc. Nat. Hist., 41, 1937: 133) states that "in recent years summer specimens have been collected in the Charleston Mountains and the Shell Creek Range." Linsdale repeated this information (1951:245). However, in his geographical summary for Nevada, Griscom (1937:161) lists no records of *grinnelli* from the Shell Creek Range, although a specimen of that race from the Quinn Canyon Range is mentioned. Because he does list an example of *bendirei* from the Shell Creek Range in his summary, it appears that there has been a confusion of localities and that there remains no basis for the recording of *grinnelli* from the same range. An unreported specimen from White Pine County, on deposit at the Museum of Vertebrate Zoology (no. 72356), was taken by H. S. Fitch on June 27, 1937, in bristle-cone pines at the head of Deadman Creek, 10,500 feet, on Mount Moriah, Snake Range. No data on gonad condition for this male were recorded by the collector. The bird is large (wing 97.9, culmen 19.1, bill depth 10.8 mm.) and it has been placed with the race *grinnelli*, with the reservation that an approach to the *benti* shape of bill is apparent.

Linsdale (1951:244–245) overlooked two records mentioned in the literature in summarizing the localities of occurrence for the species in Nevada, that of Bond for Wilson Peak, Lincoln County (Condor, 42, 1940:221) and that of Miller for the Pine Forest Mountains, Humboldt County (Auk, 52, 1935:468).

It is apparent from the information presented here that our understanding of the distribution of the species in Nevada is based in large measure on records of vagrant and non-breeding birds. An appraisal of the extent of intergradation of the races *grinnelli, bendirei,* and *benti* in the Great Basin region awaits the further collection of birds decisively known to be on their breeding grounds.

The author is indebted to Alden H. Miller for the opportunity to present the records from Elko County, to Ira La Rivers of the University of Nevada for arranging transportation to the Big Meadows area, and to John S. Spencer for assistance in the field.—Ned K. Johnson, *Museum of Vertebrate Zoology, Berkeley, California, September 24, 1957.*

Jungle and Domestic Fowl, Gallus gallus, in the Philippines.—The following notes are of our impressions, rather than systematic observations, of a situation interesting enough to put on record. In appearance many domestic fowl differ from jungle fowl only in detail, but recent introductions of modern domestic breeds have resulted in variegated birds. The jungle fowl lives on large and medium-sized islands in forest, extensive bamboo areas, and forest edge, and it forages into adjacent fields. It returns to forest trees to roost and it is a wild, shy bird. The domestic bird is widespread, co-extensive with settlement, lives about Filipino houses, where it is fed, and forages into nearby fields. It roosts near or under houses and it is very tame. Interbreeding takes place occasionally; this is sometimes arranged by man to vitalize strains of fighting cocks, and it is sometimes natural. However, in our experience, there are no half wild populations of intermediate habitat such as one would expect if the birds interbred freely.

On Siquijor Island, now largely settled, the progressive destruction of the forests has presumably eliminated the jungle fowl from most of the island. We found it only in the largest block of forest, an area of 500 hectares in rugged territory. The jungle fowl was absent from the next largest forest, an apparently suitable block of 400 hectares on fairly level ground. Perhaps this is an indication of the smallest area of habitat jungle fowl can occupy. It is noteworthy that the jungle fowl is absent from very small islands. By contrast, the domestic fowl can thrive in a dooryard and its immediate surroundings.

The domestic and the jungle fowl are conspecific; probably both descended from the red jungle fowl of India. The domestic fowl, probably more than 3000 years old, has been carried by man over most of the temperate and tropical parts of the world. But a wild type has been introduced, or established by feral birds reverting to a jungle fowl type, only locally in the Malay-Pacific area. In the Pacific area also, there are jungle fowl with an admixture of domestic breeds, and in parts of southern Asia there are half-wild, mixed populations. However, in the Philippines the two forms exist, side by side, each widespread, as though they were each phylogenetically more closely related within them-

selves than to each other. They may represent different colonizations or introductions. Now they seem equivalent to two ecological subspecies kept apart by habitat preferences. Perhaps heritable wildness versus tameness is the controlling factor. The fact that one strain has been developed by man does not make it less real. These fowl in the Philippines seem to present a model of how ecological speciation can take place.—D. S. RABOR, *Silliman University, Dumaguete, Negros, Philippine Islands,* and A. L. RAND, *Chicago Natural History Museum, Chicago, Illinois, November 12, 1957.*

A Correction in Identification of the Zone-tailed Hawk as a Mexican Black Hawk.—In the Condor (59, 1957:143), a northern breeding record for the Mexican Black Hawk (*Buteogallus anthracinus*) in New Mexico was reported. A follow-up study was made in this same nesting area in the following year, 1957.

An adult female was collected August 23, 1957, at the conclusion of nesting, and it is now identified as a Zone-tailed Hawk (*Buteo albonotatus*) rather than as a Mexican Black Hawk. This bird was identified by J. Stokley Ligon, Carlsbad, New Mexico, and is now in his collection, numbered 2029.

Between April 11 and August 23, 1957, the nest in a ponderosa pine, occupied by hawks in 1956, was observed periodically by the authors. The same nest platform was used again in 1957 with dead branches, fresh limbs of skunk brush, and *Ribes* added. On April 11, one adult was found near the nest site, and it was presumed that a second bird was also in the area. On April 27, the female flushed from the nest; on May 13, the nest was inspected and it contained two well-incubated eggs; on June 26, two fuzzy white young hawks were in the nest. Only one young survived to leave the nest. The adult female was taken on August 23 to document the species identification. The juvenile and the adult male were still present in the area at the date of collection. No further check was made of the remaining birds.

The northernmost published record of the Zone-tailed Hawk in New Mexico was reported from southwestern New Mexico near Fort Bayard on May 21, 1911, by Mrs. Bailey (Birds of New Mexico, 1928:166). Cited also in Bailey, one Zone-tailed Hawk was noted August 8, 1901, in Turkey Canyon of the Guadalupe Mountains, just a few miles from the New Mexico border inside Texas. This species has been seen in New Mexico in recent years in the White and Capitan mountains, Otero and Lincoln counties, more than in any other area (letter from J. Stokley Ligon, November 1, 1957). In the same letter, Mr. Ligon stated that Mr. V. Montgomery of Roswell, New Mexico, had seen two hawks, August 15, 1957, in the Pine Lodge area on the northeast slope of the Capitan Mountains.

The nest discovered in Mills Canyon, seven miles west of Mills, Harding County, in 1956, and under more detailed observation in 1957, indicates a sizeable northern extension of the previous range of this bird. The airline distance from Fort Bayard to the nest site in Mills Canyon is 307 miles northeast. The second most northern sight record, the Pine Lodge area in the Capitan Mountains, is approximately 175 miles slightly southwest from Mills Canyon. From these observations, it can be tentatively concluded that the Zone-tailed Hawk may soon be reported from new northern New Mexico locations.

We are indebted to Richard Johnston, Joe T. Marshall, Jr., George Sutton, and Alexander Wetmore, whose interest in the earlier Condor article led to further analysis of the identification of this hawk.—WAYNE H. BOHL and ELMO TRAYLOR, *New Mexico Department of Game and Fish, Santa Fe, New Mexico, November 27, 1957.*

Specific Relationships in the Genus Elanus.—As many as five species have been recognized within the kite genus *Elanus* (Mathews, Birds of Australia, vol. 5, 1916:205). The generally accepted treatment of the genus is that of Peters (Birds of the World, vol. 1, 1931:192–193), who recognized seven forms divided among four species (other subspecies have been described or revived in subsequent years). Of all of these forms, only two, the Australian *notatus* and *scriptus,* are sympatric. The latter differs not only from *notatus* but from all the other forms in a number of characters, some of which will be discussed here. I have examined all the forms of this genus, including the unique type of *wahgiensis* Mayr and Gilliard, in the American Museum of Natural History. Omitting *scriptus,* the situation is one of a widely-ranging group of allopatric, geographically-replacing forms. Most of the authors who have written of *Elanus* have mentioned the striking similarity of all forms, particularly between the Australian *notatus* and the American *leucurus* (cf. Hartert, Die Vögel der Paläarktischen Fauna, vol. 2, 1914:1185). The differences among this group of forms are all relatively minor, involving principally size, shade of gray of the upper parts, and degree of development of the

pattern of the under side of the wing. In any of these characters, the forms may be arranged in a progressive intergrading series. None of them is separated from any other by differences approaching the extent of those between the sympatric *notatus* and *scriptus*.

Mayr, Linsley, and Usinger (Methods and Principles of Systematic Zoology, 1953:104) conclude a lucid discussion of the problem "Subspecies or Allopatric Species?" by stating that "the use of trinomials conveys two important pieces of information: (1) closest relationships and (2) allopatry . . . . To treat such allopatric forms as separate species has few practical advantages." I believe that this principle is exceptionally well illustrated in *Elanus*. The distinctiveness of *scriptus* from the sympatric *notatus* and from all other members of the genus strongly suggests that all of the latter are more closely related to one another than any is to *scriptus*. In order to express these degrees of relationship, the logical step would be to combine all these geographically replacing forms into a single species under the oldest name, *Elanus caeruleus*, leaving *E. scriptus* as the only other species in the genus. As suggested by Mayr, Linsley, and Usinger (and many others), taxonomic judgment must be substituted for concrete evidence of conspecificity in these strictly allopatric forms; it may be pointed out in this connection that the various races here assigned to *Elanus caeruleus* resemble one another more closely than do some of those currently accepted as belonging to single widely ranging falconiform species (for example, *Accipiter gentilis*, *Accipiter striatus*, *Falco peregrinus*, and others).

The species *Elanus scriptus* is confined to Australia, where it overlaps the range of *E. caeruleus notatus*. Condon and Amadon (Records of the South Australian Museum, 11, 1954:193–196) have published good comparative descriptions of the two species. One of the distinguishing characters they use needs to be somewhat modified. They state (p. 194) that the small outer primary of *scriptus* differs from that of *notatus* in being uniformly gray rather than "white on the outer web and gray on the inner." Actually the feather in question is, in *notatus*, gray on both webs, but it has a white edge which is obsolete or absent on the inner web and fairly well developed on the outer web. In *scriptus*, only the tip is white. The various races which I propose to combine into *caeruleus* all have the *notatus* pattern with various degrees of development of the white edge.

A good distinguishing character for the two sympatric species of *Elanus* in Australia, not mentioned by Condon and Amadon, lies in the fact that in *E. scriptus* the shafts of all the white tail feathers (that is, all rectrices except the central pair) are white; in *E. c. notatus* these shafts are dark. This is not, however, a specific character for *E. caeruleus* throughout its range; in *E. c. hypoleucus* and *E. c. intermedius*, the shafts of the white rectrices are white, except that in some individuals the shafts of the innermost white rectrices are somewhat darkened. In other races of *E. caeruleus*, the shafts of the outermost pair of rectrices are frequently white.

Unlike Condon and Amadon, I would interpret the similarity of the Australian *notatus* to the American *leucurus*, and the distinctiveness of the Australian *scriptus*, as evidence that the latter, not the former, was the earlier arrival in the putative "double invasion" of Australia by *Elanus*. I have discussed this with Dr. Amadon, and he is now inclined to agree with this interpretation.

Salomonsen (Vidensk. Medd. Dansk Naturh. Foren., 115, 1953:209–210) has recently reviewed the races of *E. caeruleus* in its former restricted sense. He synonymized *intermedius* Schlegel with *hypoleucus* Gould. However, Javanese specimens are quite noticeably paler gray above, particularly on the crown, than are Philippine and Celebes specimens. I believe that *intermedius* is worthy of recognition for the Black-winged Kite population of Java.

The following arrangement of the species and subspecies of *Elanus* is proposed:

Elanus caeruleus caeruleus (Desfontaines)
vociferus (Latham)
sumatranus Salomonsen
hypoleucus Gould
intermedius Schlegel
wahgiensis Mayr and Gilliard
notatus Gould
leucurus (Vieillot)
majusculus Bangs and Penard
Elanus scriptus Gould.

—Kenneth C. Parkes, *Carnegie Museum, Pittsburgh, Pennsylvania, August 28, 1957.*

Red-tailed Hawk Feeds on Crickets.—On January 14, 1957, William B. Bradford of the California Department of Fish and Game brought a Red-tailed Hawk (*Buteo jamaicensis calurus*) to the California Academy of Sciences. The bird had been shot the previous day by an unidentified person near Castle Rock, Corral Hollow, San Joaquin County, California. It was an immature female, just beginning to assume adult plumage, and it proved to be unusually fat, weighing 1098.5 grams. An examination of its digestive tract revealed the remains of 49 Jerusalem crickets (*Stenopelmatus fuscus*). Seventeen of these were in the crop and 32 were in the stomach. No other food material was present. All of the crickets were fairly intact, indicating that they had been ingested not long before the bird was shot.

Although Red-tailed Hawks are known to capture crickets occasionally (Bent, U. S. Nat. Mus. Bull. 170, 1938), the presence in the crop and stomach of a diurnal bird of prey of such a large number of nocturnal insects that live fairly deep in the ground during the daytime seemed rather unusual. Correspondence with William Bradford revealed that he had observed concentrations of Red-tailed and Marsh hawks, on January 13, in the vicinity of alfalfa fields near the town of Tracy which is 7½ miles northeast of Castle Rock. Many of these fields had recently been flooded with irrigation water to offset the drought that prevailed through much of the mid-winter in California. Since flooding generally forces crickets from their subterranean hiding places it appears possible that these man-made inundations may have been responsible for unearthing these insects, thereby providing certain hawks in the vicinity with a type of food that is usually inaccessible to them.—ROBERT T. ORR, *California Academy of Sciences and University of San Francisco, San Francisco, California, October 23, 1957.*

Repeated Attacks by a Sharp-shinned Hawk on a Pileated Woodpecker.—Seven attacks made within 10 minutes by a Sharp-shinned Hawk (*Accipiter striatus*) on a Pileated Woodpecker (*Dryocopus pileatus*), observed near Seneca, Maryland, on October 5, 1957, were interesting from the point of view of the behavior of both birds involved. At 8:00 a.m. I approached a dead elm by the Chesapeake and Ohio Canal, on the look-out for Pileated Woodpeckers. In previous months, I had seen at least one of them come to drum on a hollow portion of the elm, or to rest and preen in early morning sunshine. On October 5, there were two Pileated Woodpeckers. One flew away, but the other, a male, crossed over to an oak on my side of the canal. Then I saw him fly back across the canal closely pursued by a Sharp-shinned Hawk. The woodpecker returned to the elm, hammered on some bark, then hitched to a high limb and drummed not too loudly; he then preened his feathers. The Sharp-shinned Hawk was perched 10 feet away on another dead limb. It suddenly flew at the woodpecker and a short pursuit followed, but the woodpecker again returned to the elm and drummed once more, this time lower down. The hawk also returned. It sat upright and motionless except for side-to-side motions of its tail. Then it attacked the woodpecker for a third time. The woodpecker dodged around the trunk but the hawk, with amazing control, banked so as to cut around the trunk also. Another chase now took place through the woods. At one point the woodpecker swooped low to the ground and the hawk, well above him, dove nearly vertically downward through the trees. Four more attacks took place in succession, hawk and woodpecker alighting, between attacks, not far apart on trees adjacent to the elm. In the last encounter, the woodpecker gave loud *cuk, cuk* notes as he circled more widely than previously but alighted near his starting point. Following the report of a shotgun, he finally flew downstream. Farther along the canal I saw two more Sharp-shinned Hawks. It seemed probable that a migratory flight of these birds was taking place.

Discussion.—Some aspects of the attacks described were surprising to the observer. The Sharp-shinned Hawk was swift and agile, banking, diving, and reaching when close with long legs and talons outstretched. In comparison the woodpecker was large and slow. This appearance, however, may have been deceptive. The Pileated Woodpecker seemed to drop out of reach at critical moments and it was not sufficiently frightened by the attacks to leave the vicinity of the elm or to refrain, in interim periods, from such activities as drumming and preening. A similar lack of concern in a Pileated Woodpecker has been described by Michael (Condor, 23, 1921:68) who watched one of these woodpeckers drilling with apparent unconcern while a Cooper's Hawk (*Accipiter cooperii*) perched within a few feet of it. In this instance, the woodpecker finally drove the hawk away. There is no reason to believe that the encounters which I witnessed by the canal were simply play, for seven attacks, driven close

to home, indicated that the hawk was trying to strike down the larger bird.—Lawrence Kilham, *Bethesda, Maryland, October 15, 1957.*

Sora, Snowy Egret, Blue-winged Teal, and Mourning Dove in Juneau, Alaska.—On October 21, 1956, a Sora (*Porzana carolina*) was collected near the Juneau airport. The specimen is the first from Alaska in the Fish and Wildlife Service collection.

On May 18, 1957, I received two reports of a bird fitting the description of a Snowy Egret (*Leucophoyx thula*) at Lemon Creek near Juneau. On May 19, four more persons reported seeing the bird. On May 20, Mr. and Mrs. E. L. Keithahn of the Territorial Museum, Game Management Agent Ralph Smith, and I observed the bird for one-half hour at close range while it fed on small fish in a shallow creek. The typical white coloration, size, plumes, black bill, legs, and light colored feet left no doubt as to its identity. The bird became quite a spectacle to the local citizens and was observed on May 22, 23, and 24.

On May 20, while seeking the egret, Mrs. Nelson and I observed a pair of Blue-winged Teal (*Anas discors*), a pair of Mallards (*Anas platyrhynchos*), and a pair of Green-winged Teal (*Anas carolinensis*) in a small pond near Juneau. The birds were in spring plumage. On July 7, 1957, a pair of Blue-winged Teal were observed at Salmon Creek. On September 1, 1957, Game Management Agent Fred Robards received reports of five Blue-winged Teal taken by hunters at Eagle River. Wings of the teal were obtained and identified as those of the Blue-winged Teal. On September 1, a Mourning Dove (*Zenaidura macroura*) was shot at Eagle River near Juneau. The specimen is being prepared for the Fish and Wildlife Service collection.—Urban C. Nelson, *Juneau, Alaska, October 30, 1957.*

Cape May Warbler in Nicaragua.—The recent note by Slud (Condor, 59, 1957:340) on the occurrence of the Cape May Warbler (*Dendroica tigrina*) in Costa Rica has prompted me to record another specimen of it from Central America. On January 13, 1957, I collected a Cape May Warbler 12 km. east of Managua, Department of Managua, Nicaragua; this locality is approximately at sea level and is on the Pacific slope of the country. The bird was feeding actively with some other passerines in a tree beside a small stream. Its skull was double-layered and the plumage appears to be that of an adult male; the testes were not enlarged. Curiously, all the individuals of this species observed by Slud in Costa Rica were also males.

This was the first Cape May Warbler that I have encountered in Nicaragua although I have observed many kinds of wintering North American warblers on both the Pacific and Caribbean slopes of the country. The scarcity of records of this species from Central America indicates that it is not common in the area, but Slud's records and the present one, which together cover a span of more than four years, suggest that this warbler may be a regular but rare winter visitant to both slopes of Central America.—Thomas R. Howell, *Department of Zoology, University of California, Los Angeles, California, October 2, 1957.*

NOTES AND NEWS

The editors call attention to a significant work in the botanical field that has recently appeared and which may be of great value to students of wildfowl. This is the book by Herbert L. Mason entitled, "A Flora of the Marshes of California." It is a superbly illustrated manual of the marsh plants and should serve as an important technical reference for all persons concerned with waterfowl management and natural history. We are not in a position technically to review this botanical work but believe it will be welcomed by ornithologists. The book is published by the University of California Press and consists of 878 pages. There are 365 figures. The volume was issued November 25, 1957, and is priced at $10.

COOPER SOCIETY MEETINGS

SOUTHERN DIVISION

SEPTEMBER.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on September 24, 1957, at the Los Angeles County Museum. The following names were proposed for membership: Alice G. Allen, 143 W. Acacia, Apt. 4, Stockton, Calif., by Ethel S. Willets; Donald G. Davis, P. O. Box 145, Timnath, Colo., by Paul H. Baldwin; John Polk Kerr, Scripps Institution of Oceanography, La Jolla, Calif., by Carl L. Hubbs; Seymour H. Levy, Rt. 9, Box 960, Tucson, Ariz., by Joe Marshall; John C. Ondrias, Museum of Vertebrate Zoology, Berkeley, Calif., by A. H. Miller; C. John Ralph, 1043 Merced Ave., Berkeley, Calif., by H. L. Cogswell; Herald H. Shoup, Middlebury, Ind., by F. A. Pitelka; Lee Silvernale, 755 N. Robinson Rd., Topanga, Calif., by W. Lee Chambers; David Armstrong West, Fernow Hall, Cornell University, Ithaca, N.Y., and William Frederick Zimmerman, 126 South Drive, Fox Chapel, Pittsburgh, Pa., by Charles G. Sibley; Dr. George A. Allen, 1328 Allen Park Drive, Salt Lake City, Utah, and Robert J. Niedrach, Box 116–A, R. R. No. 3, Littleton, Colo., by Ed N. Harrison; Chas. S. Jones, 555 S. Flower St., Los Angeles, Calif., W. Alton Jones, 1 Sutton Place South, Apt. 8–A, New York, N.Y., and C. R. Smith, 510 Park Ave., New York, N.Y., by J. R. Pemberton; John Jewet Garland, 117 W. 9th. St., Los Angeles, Calif., Wm. T. Sesnon, Jr., 612 S. Flower St., Los Angeles, Calif., and Clyde G. Smith, 9739 Guatemala, Downey, Calif., by W. J. Sheffler; Mrs. Vance Phillips, 1010 Monte Drive, Santa Barbara, Calif., James O. Seamans, Alcott Road, Concord, Mass., and James R. Travis, 4498-B Fairway, Los Alamos, New Mexico, by Frank H. Boynton; John M. Gates, Cooperative Wildlife Research Unit, Utah State University, Logan, Utah, Mr. Seima Matsui, % Kamo Norin Koto-Gakko, Jyojo, Kamo-Shi, Niigata-Ken, Japan, H. H. Singleton, 1236 So. 2nd St., San Jose, Calif., Ronald LeRoy Walker, P. O. Box 1761, Hilo, Hawaii, by Jack C. von Bloeker, Jr.; Murray Abowitz, M.D., 6333 Wilshire Blvd., Los Angeles, Calif., Sydney Anderson, Museum of Natural History, University of Kansas, Lawrence, Kans., T. K. R. Bourns, Dept. Biology, Queen's University, Kingston, Ontario, Canada, Samuel Renick Chamberlain, Refugio, Texas, Ben B. Coffey, Jr., 672 N. Belvedere, Memphis, Tenn., Gordon Curtis, 1391 Franklin St., Santa Clara, Calif., Mrs. Roy N. Dickie, 3840 Loquat Ave., Miami, Fla., Cora L. Evans, 1444 Calhoun St., New Orleans, La., Harry S. Fasnacht, Union Deposit, Pa., Bernard Feinstein, 506 "A" St., N.E., Washington, D.C., Mrs. Thomas Fleming, 1541 Lombardy Rd., Pasadena, Calif., John Edmond Galley, 1610 Holloway Ave., Midland, Texas, Brother Gines, Sociedad de Ciencias Naturales La Salle, Apartado 681, Caracas, Venezuela, James K. Guthrie, The Sun Company, San Bernardino, Calif., Mrs. Neil Haig, 2216 Federal Ave., Seattle, Wash., Palmer D. Miller, M.D., 1063 N. Fulton St., Fresno, Calif., Mrs. Ernest M. Pace, Jr., 627 S. Windsor Blvd., Los Angeles, Calif., A. J. Penick, 6344 Brompton, Houston, Texas, Robert M. Stabler, Colorado College, Colorado Springs, Colo., and Raymond R. Stefanski, Armstrong Creek, Wis., by C. V. Duff; Richard E. Woodard, 2050 Torrey Pine Rd., La Jolla, Calif., by Thomas R. Howell.

On August 13, Arnold Small observed two Black-footed Albatrosses, 35 Black Petrels, and one Skua off the southeast end of San Clemente Island. On August 24, at Mt. Pinos on the day of the fire in the Cleveland National Forest, he saw 25 to 30 Condors; 17 of them were in view at one time. Small also reports a moderately good flight of Elegant Terns off the southern California coast. On August 25 he observed one female Black Scoter and one Osprey at Malibu, and 2500 Sooty Shearwaters off Point Dume.

On August 28, 29, and 30, while with the U. S. Navy on maneuvers between San Diego and San Clemente Island, Ben King, Jr., saw 19 Black-footed Albatrosses, 75 Black Petrels, 20 Leach's Petrels, 2 Ashy Petrels, 1 Sabine's Gull, 1 Skua, 1 Tropic Bird, and 20 Xantus' Murrelets. Later,

on September 9, on a trip from San Pedro to approximately 25 miles south of San Clemente and 50 miles off the mainland coast, he saw 75 Elegant Terns, 3 Arctic Terns, 8 Common Terns, and 5 Red-billed Tropic-birds.

Dr. R. A. Boolootian of the Department of Zoology, University of California at Los Angeles, showed his fine colored motion picture, "Habits and Behavior of the California Sea Otter."—DOROTHY E. GRONER, *Secretary*.

OCTOBER.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on October 29, 1957, at the Los Angeles County Museum. The following names were proposed for membership: Prof. F. Bourliere, 15 Avenue de Tourville, Paris 7, France, by Thomas R. Howell; J. E. Boyd, 3640 Los Feliz Court, Riverside, Calif., and Irving Kassoy, 235 S. 4th St., Columbus, Ohio, by C. V. Duff; James S. Fassero, 4622 Loleta Ave., Eagle Rock, Calif., Derek T. Lees-Smith, Broadmoor Hospital, Crowthorne, Berkshire, England, and Robert Garr Mayne, 312 N. Commonwealth Ave., Los Angeles 4, Calif., by J. C. von Bloeker, Jr.; Stanley B. Hare, 2505 Canyon Oak Dr., Hollywood 28, Calif., by Kenneth E. Stager; Glen L. Kashin, 61 "T" St., Salt Lake City 3, Utah, by Mrs. Stanton Tainter; and Dr. Robert M. Stabler, Colorado College, Colorado Springs, Colo., by F. H. Boynton.

Roland C. Ross reported having seen 40 Surfbirds at Playa del Rey on October 21. Earle Greene reported that 100 Elegant Terns were still at Malibu Creek on October 19. Dorothy Groner saw an Eastern Phoebe at Squaw Flat in Little Sespe Canyon on October 27.

"Fat Deposition in Relation to Migration" was the subject of speaker Dr. Eugene Odum, Department of Zoology, University of Georgia.—DOROTHY E. GRONER, *Secretary*.

NOVEMBER.—The monthly meeting of the Southern Division of the Cooper Ornithological Society was held on November 26, 1957, at the Los Angeles County Museum. The following names were proposed for membership: Mrs. Paul W. Hiller, 6436 Via Canada, San Pedro, Calif., by C. V. Duff; Leonard J. Peyton, R.F.D. No. 2, Box 260, Fillmore, Calif., by Jack C. von Bloeker; John G. Sarles, 3403 Pine Crescent, Vancouver 9, B.C., Canada, by F. H. Boynton; Prof. Dr. Ernst Schuz, Naatl. Museum fur Naturkunde in Stuttgart, Stuttgart-O, Schloss Rosenstein, West Deutschland, by T. R. Howell; and John R. Stevens, Dept. of Life Sciences, Los Angeles City College, Los Angeles 29, Calif., by A. H. Miller.

Gerhard Bakker reported that a hibernating Poorwill had been brought to him by a student at Los Angeles City College. Among recent observations made by Arnold Small were: Oct. 5th, on a boat 12 miles west of Monterey, 1 Cassin's Auklet, 3 Xantus' Murrelets, 2 Rhinoceros Auklets, 1 Black-footed Albatross, 4 New Zealand Shearwaters, 2 Slender-billed Shearwaters, Skuas sighted 10 times, with 3 in sight at once, 40 Pomarine Jaegers, 26 Parasitic Jaegers, at least 300 Ashy Petrels, and 40 Black Petrels; on Oct. 5th, at the mouth of the Salinas River, 1 Golden Plover; on Nov. 9, at the Ventura County Gun Clubs, at least 50 Starlings; and on Nov. 2, as far as 50 miles south and west of Newport Beach and circling San Clemente Island, 3 New Zealand Shearwaters, 30 Black Petrels, and 50 Ashy Petrels. Ed N. Harrison reported that while he was on a fishing trip between La Paz and Cape San Lucas during the week of Nov. 18, many unidentified petrels followed the boat and appeared to land almost in the wake and on the backs of the marlin. W. J. Sheffler, while at San Quintín Bay, Baja California, between November 21 and 24, found that Black Brant had arrived early this year and were abundant. Scaup were present in flocks of 300 to 700, Hooded Mergansers in groups of 2 to 6, and Common Mergansers in groups of 12 to 15. He also found that Buffleheads were more abundant there so far this year.

Sidney B. Peyton showed a fine collection of colored slides taken on his trip in early summer to Old Crow and the vicinity of the Porcupine River, Yukon Territory.—DOROTHY E. GRONER, *Secretary*.

For Sale, Exchange, and Want Column—Each member of the Cooper Society is entitled to one short advertising notice in any issue of the Condor free. Notices of over 3 lines will be charged for at the rate of 25 cents per line. Send advertising copy to Jack C. von Bloeker, Jr., Los Angeles City College, 855 N. Vermont Ave., Los Angeles 29, California.

WANTED—Preserved avian specimens, just hatched, all species, identified, maximum 12 hours old. —DAVID K. WETHERBEE, *Pomfret Center, Hampton, Conn.*

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WANTED—Graduate student wants to buy Nice, M. M., Studies in the Life History of the Song Sparrow, parts I and II; Beach, F. A., Hormones and Behavior; and Strong, R. M., A Bibliography of Birds, parts I, II, and III.—JERRAM L. BROWN, *Museum of Vertebrate Zoology, Berkeley 4, Calif.*

WANTED—Griscom, Ornithology of Guerrero; and Peters, Birds of the World, vols. 1–7. Please state price and condition.—DON R. MEDINA, *Museum of Vertebrate Zoology, Berkeley 4, Calif.*

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DISTRIBUTIONAL CHECK-LIST OF THE BIRDS OF MEXICO

PART II

The Cooper Ornithological Society announces the publication on December 20, 1957, of Part II of the Distributional Check-list of the Birds of Mexico as Pacific Coast Avifauna No. 33.

This work, which contains 436 pages, is the concluding part of the Mexican Check-list. Part I was published in 1950 as Pacific Coast Avifauna No. 29. Part II deals with the families from the Trogonidae to the Fringillidae. Thus the first complete list of Mexican birds is now available. For each species and subspecies the detailed occurrence in México is recorded by states, based on records in the literature and on a wealth of available museum specimens. Seven color plates from Grayson's historic paintings of Mexican birds are included.

Part II has been completed by a group of author-compilers of which Alden H. Miller has served as Editor-in-chief and Herbert Friedmann, Ludlow Griscom, and Robert T. Moore as Co-editors.

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